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BULLETIN
OF THE
TORREY BOTANICAL CLUB

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The Mechanics of Conidial Fertilization in Neurospora sitophila

MYRON P. BACKUS[1]

(WITH PLATES 1 TO 4 AND ONE FIGURE)

Neurospora sitophila Shear and Dodge is a heterothallic ascomycete with a *Monilia* imperfect stage. Single ascospore isolates have been found to fall into two reaction groups commonly designated as "A" and "B." Although sclerotial bodies (incipient perithecia) may be produced on isolated thalli of both reaction groups, it is only when an A strain is mated with a B strain that mature ascocarps are obtained.

In a paper published in 1932 Dodge (5) described experiments demonstrating that the microconidia produced by *N. sitophila* may act as fertilizing agents. When a suspension of microconidia from one strain was applied to the sclerotial bodies on a plate culture of a strain of the opposite reaction, these incipient perithecia in the localized areas to which microconidia were applied promptly developed into normal perithecia which matured spores. Further experiments made clear that a suspension of ordinary monilioid conidia (macroconidia) could be substituted for the microconidia and that these macroconidia are even more effective as "spermatizing agents." The writer had the privilege of witnessing the above-mentioned experiments and has himself since then many times conidiated plate cultures of *N. sitophila* and watched the remarkably rapid transformation of the sclerotial bodies into perithecia in the conidiated areas (1).

Dodge and Swift (9) suggested that some of the hair-like outgrowths which may be seen protruding from the sclerotial bodies when one looks down on a plate culture with a low-powered microscope, might be receptive hyphae. Later, as a result of study of stained sections of incipient

[1] This investigation was carried on during the summer of 1937 with the aid of a grant from The Wisconsin Alumni Research Foundation.

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perithecia in monosporous cultures of *N. sitophila*, Dodge (6) was able to demonstrate that trichogynous hyphae actually are formed, taking their origin from various cells of the ascogonium. He concludes that "there can be no doubt that when one applies either the orange-colored monilioid conidia or the microconidia artificially, these trichogynous outgrowths are the means by which nuclei of the other sex are brought into the ascogenous cells." The fusion of microconidia or of macroconidia with these extensions from the ascogonium, was, however, never observed.

The present study is an extension of this line of investigation; it has brought to light some further details concerning the mechanism of fertilization in *N. sitophila*. In this work only three strains of the fungus were employed: an albino (non-conidial) "A" strain, "56.6," a conidial "B" strain, "56.4," and a conidial "A" strain, "56.8." These were kindly supplied by Dr. B. O. Dodge. For the pedigree of these races the reader is referred to Dodge's original account (4), pp. 11–13.

THE YOUNG SCLEROTIAL BODY

To study the initial stages in the development of sclerotial bodies, cover glasses were placed directly on the agar surfaces of 48-hour-old plate cultures of strain 56.6. It was thus possible to observe under high magnification the manner in which the incipient perithecium originates and to follow the early stages of its development. The essential points observed in this connection are the following: Each sclerotial body begins as a more or less helically coiled hypha originating from one of the vegetative hyphae of small diameter. The coil soon becomes septate, and from its lower part grow out branches which initiate the sterile covering that comes to consist of a dense intertwining mass of threads.

Microtome sections of fixed material stained in iron-alum haematoxylin revealed the ascogonium to be made up of a short coil of cells of greater diameter than the cells of the envelope and more readily staining. The ascogonium appears to be the terminal part of the original helical outgrowth. The fertile cells are of various sizes, but all are multinucleate. Some of the nuclei of the fertile cells are rather consistently much larger than others, even in the same cell, and both large and small nuclei occasionally show a paired arrangement. Until considerable growth of the sclerotial body has occurred, the fertile coil ends blindly and remains enveloped by the sterile sheath. Only later do trichogynous extensions grow out.

All these observations are in approximate agreement with the account given by Dodge (6).

TRICHOGYNE-CONIDIUM RELATIONS

In an attempt to study the trichogyne system and the relations which, according to Dodge's hypothesis, this system must establish with conidia of the opposite reaction placed upon the agar surface, the conventional approach of sectioning and staining fixed material was first employed. Blocks of agar from marked conidiated areas of plate cultures were fixed at intervals of two hours over a period of approximately two days. Study of this material, however, gave only a fragmentary picture of the trichogynes; and although conidia were recognizable in the finished slides, no spores were seen attached to receptive hyphae. A technique yielding much better results was soon substituted.

It was found that the mycelium of strain 56.6 could be induced to grow across a sterile glass slide placed on the surface of the agar in a petri dish. The inoculum was placed on one side of the dish and the slide directly in the middle. The cultures were incubated at 23°C. and at this temperature not only did the hyphae seem to grow over the slide readily, but formed an abundance of sclerotial bodies there. Test conidiations showed that perithecial development identical with that occurring on agar could be obtained on the surface of the glass. Series of cultures of race 56.6 were therefore started on corn-meal agar. When sclerotial bodies appeared on the mycelium which had grown over the glass, a conidial suspension was prepared from a young culture of strain 56.4. This suspension after being filtered through several layers of sterile filter paper was painted over the surface of the slides with a delicate camel's hair brush. The cultures were then returned to the incubator. At two hours following, slides were removed from the dishes, cotton blue dissolved in lacto-phenol was applied with a pipette, and cover glasses were added. After suitable staining, the excess cotton blue was washed out by drawing clear lacto-phenol under the cover glass by means of a blotter. Preparations so made gave a full picture of the trichogynes and also made clear the associations of these with the conidia introduced. When one examines with a microscope the surface of a young plate culture of *Neurospora* there is no way of distinguishing the trichogynes among the numerous sterile hyphae which grow out from the surface of the sclerotial body at about the same time as the trichogynes. In the cotton blue preparations, however, the differential staining obtained not alone revealed the ascogonium clearly in the young sclerotial body, but also made the trichogynous outgrowths from it stand out so well that they were readily traced throughout their entire extent.

The fully developed trichogyne system of certain sclerotial bodies was found to be remarkably extensive, consisting in some cases of two or three

branching trichogynes arising from several cells of the ascogonium. If, as is occasionally the case, a single trichogyne is present, this appears to be simply an extension from the tip of the ascogonial coil. Instead of a simple prolongation of the coil, however, there may be a forking of the end cell and two trichogynes growing out. A trichogyne may give rise to a branch before leaving the pseudoparenchymatous envelope of the sclerotial body, this branch then apparently burrowing its way to the exterior independently. Each trichogynous branch after emerging from a sclerotial body may in turn send out one or more ramifications. In addition to the extensions from the terminal region there may also be in the more complicated cases a trichogyne arising from the penultimate or antepenultimate cell of the ascogonial coil. Figures 1, 2, and 4 illustrate some of the variations met with. The longest single trichogynous hypha encountered was 750μ long; and the total length of the most extensive trichogyne system—adding up the lengths of all branches—was 2000μ. The trichogynes are in general very slender, have occasional cross walls, and usually taper gradually toward their distal ends. On the whole they are of smaller diameter than the hair-like outgrowths from the superficial cells of the sterile covering of the incipient perithecium or than any other hyphae in the field. Dodge (6) described presumably receptive hyphae growing to the outside from the basal part of the ascogonium. Such hyphae could not be identified in the preparations made as here described.

Probably because of the presence of some inhibiting substance produced in the metabolism of the mycelium, conidia which are placed on the agar or glass surfaces across which hyphae have grown do not germinate. The conidia placed on the glass slides as previously described stain even more intensely than the trichogynes, so that they are readily recognizable, but no signs of germination were observed.

Beginning about 4 hours after conidiation fusions between conidia and trichogynes were evident. Whether it is a matter of trichogynes by chance encountering the conidia, or whether a chemotropic attraction exists which causes the trichogynous branches to seek out, as it were, the conidia, is not clear. Although there is some reason for suspecting a chemotropic response on the part of the trichogynes, the evidence is yet inadequate to justify a definite conclusion. In any case it is primarily terminal portions of the trichogyne which are receptive. Very often the tip of a long trichog-

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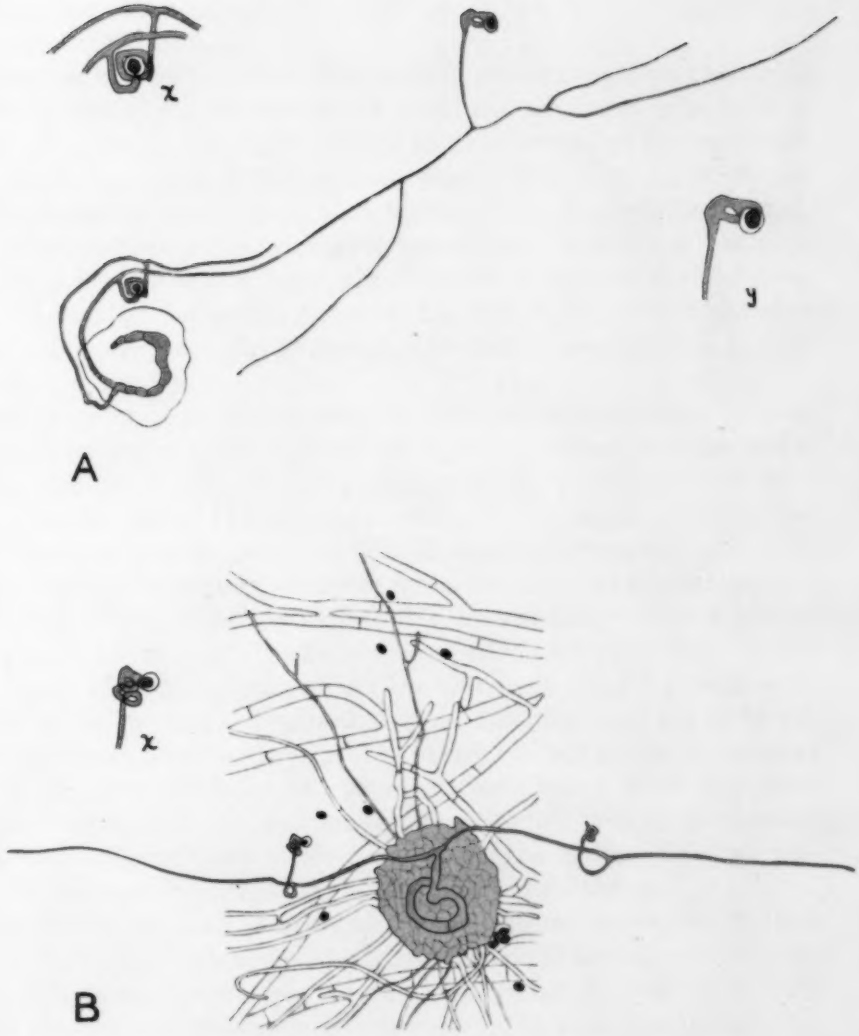
Explanation of Plate 1

Fig. 1. A and B. Trichogyne-conidium relations in *Neurospora sitophila*, nine hours after conidiation. x and y detail of union of trichogynous hyphae with conidia. Camera lucida sketches. Large figures × 170; x and y × 340.



BACKUS: NEUROSPORA FIG. 1

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ynous branch was seen to have fused with a conidium. Sometimes, however, it was a short lateral branch that was involved, its development possibly induced by the presence of the conidium in the near vicinity. In only one case observed had a non-terminal portion of a trichogyne fused with a spore (Fig. 2, A, x).

Upon the approach of the trichogynous hypha to a conidium frequently the end of the hypha becomes much coiled and contorted (Fig. 1, B, x; Fig. 2, A, y and z). Sometimes several short processes are put out which wrap about the conidium like so many fingers (Fig. 1, A, y); or the end of a trichogynous branch may wind tightly about the conidium (Fig. 1, A, x). The portion of the trichogyne immediately adjacent to the conidium may become several times the diameter of the rest of the hypha. Some hours after fusion has occurred, the wall in the thickened region frequently swells markedly as though a process of gelatinization had set in (Fig. 3, B and C).

Shortly after contact, a cytoplasmic connection is established between the conidium and the trichogyne in the region of contact; and the protoplasmic content of the conidium begins to enter the trichogyne (Figs. 1 and 2). By the end of 12 hours after conidiation the major portion of the conidial protoplasm has passed in (Fig. 3); but total evacuation of a conidial wall has not been observed. Although nuclei could not be distinguished in the type of preparation employed, it is evident that at least a portion of the nuclei of the multinucleate conidium must have entered the trichogyne along with the cytoplasm, *via* the extremely slender protoplasmic bridge. While the actual details of nuclear migration have yet to be followed, there can be no further doubt as to how nuclei reach the ascogenous area in the sclerotial body. In case a relatively heavy spore suspension was used in conidiation, it was not uncommon to find three or four conidia fused with different parts of the same trichogyne system, although presumably fusion with one conidium should assure fertilization.

By the end of 12 to 15 hours at the temperature employed, the first definite signs of growth of the sclerotial bodies could be observed with the aid of a binocular microscope. We may assume that the migration of the nuclei through the trichogyne is relatively rapid, and that probably at the time gelatinization of the walls of the portion of the trichogyne near the attached conidium was observed, the conidial nuclei had already entered the ascogonium, thus providing the necessary stimulus for the development of the sclerotial body into a perithecium. The gelatinization of the trichogyne walls thus probably represents a degeneration phenomenon. That nuclei from conidia actually enter the ascogonium is attested by Dodge's observation, which the writer has confirmed, that asci from peri-

thecia induced to form through conidiation contain both "A" and "B" ascospores.

Although in *Neurospora* hyphal fusions are common between vegetative hyphae, and although sterile hyphal outgrowths from the surface of the young perithecium have frequently been seen to fuse with one another or with similar outgrowths from near-by perithecia or even with ordinary vegetative hyphae of the parent culture, no case of fusion of any portion of the trichogyne system with such hyphae has been disclosed by a relatively careful search. Furthermore, in a single trial involving a considerable number of preparations, no evidence was found of union of trichogynes with conidia, when conidia of the same reaction (A) from strain 56.8 were used in conidiating plate cultures of strain 56.6.

In a renewed attempt to study the receptive apparatus in stained sections, thick sections were cut parallel to the surface of the agar. A few preparations were obtained showing a portion of a trichogyne which could be traced back to the fertile coil. Branching and attachment of conidia were seen. These preparations are valuable chiefly in making it clear that the situation observed when the development takes place on a glass surface, is a true picture of what occurs when the fungus is growing on an agar medium.

LOCALIZED DEVELOPMENT OF PERITHECIA

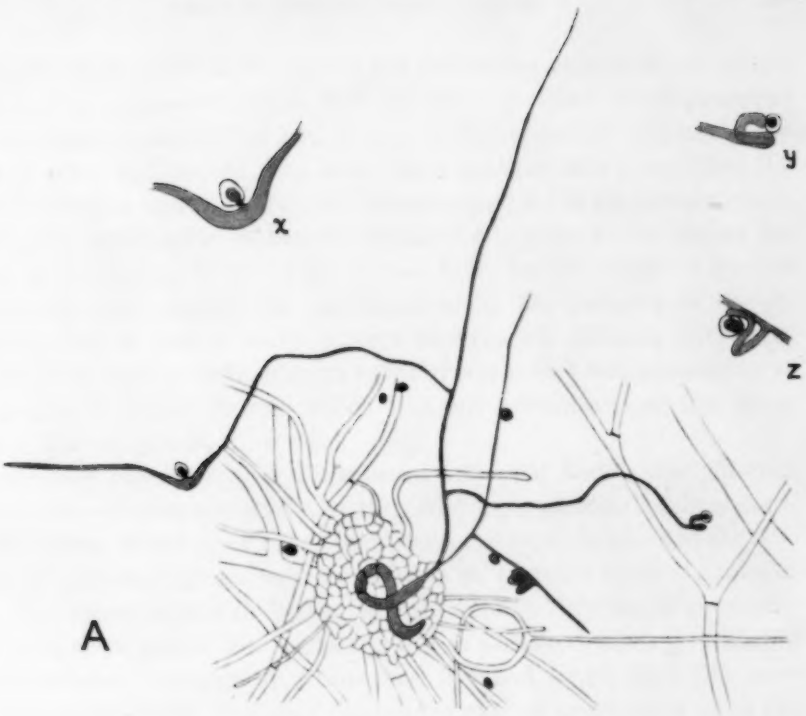
The above account of trichogyne-conidium relations suggests why localized development of perithecia results when conidia of the appropriate reaction are placed on sclerotia-covered areas of *N. sitophila* cultures. Localized development of perithecia may, however, be obtained in a variety of ways. This is evident from the results of the experiments now to be described.

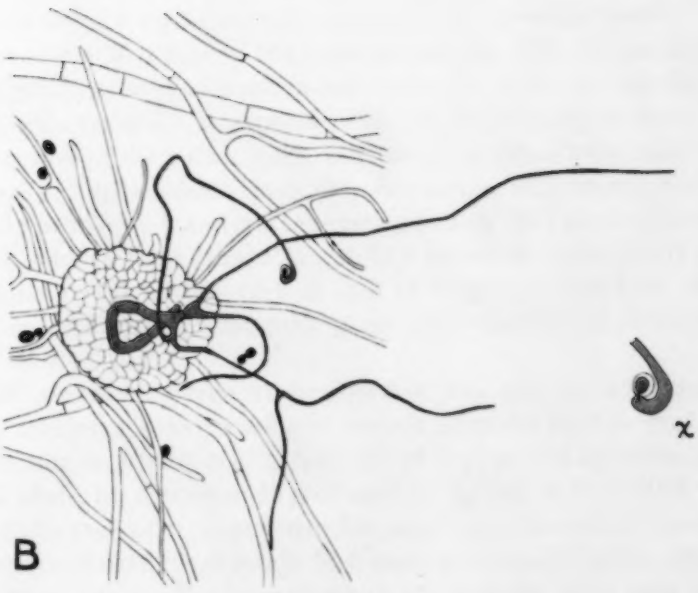
Droplets of a filtered conidial suspension of strain 56.4 were applied to young cultures of strain 56.6 in marked areas wherein the mycelium had grown but where no sclerotial bodies had yet developed. As previously pointed out, conidia do not germinate when placed on areas occupied by mycelium. As soon as sclerotia were formed fertilization was effected; and the same localization of perithecia was obtained as if spores had been placed on sclerotia-bearing regions.

Strain 56.6 is a rapidly growing race. This is important in considering the results of the next experiment. When conidia of strain 56.4 were placed

Explanation of Plate 2

Fig. 2. A and B. Trichogyne-conidium relations in *N. sitophila*, nine hours after conidiation. x, y, and z detail of union of trichogynous hyphae with conidia. Camera lucida sketches. Large figures ×200. x, y, and z ×400.





BACKUS: NEUROSPORA FIG. 2

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on the clear agar just a little beyond the advancing margin of the mycelium in a plate culture of strain 56.6, the same localized development of perithecia again occurred—although these bodies appeared only about the third day after conidiation, i.e., after the mycelium had penetrated the area and sclerotia had been formed. Observations made on certain plates following the application of conidia revealed a portion of the spores beginning to germinate. Within a few hours, however, the vigorous hyphae of strain 56.6 had crossed the conidiated area. The presence of the invading hyphae of course made further observation difficult but, in so far as could be seen, growth of germ tubes of strain 56.4 was arrested or at least greatly inhibited. Spores which had not germinated at this stage probably did not germinate at all.

In another experiment fertilization of sclerotial bodies was effected with germinated spores. Conidia of race 56.4 were germinated in a corn-meal decoction. When germ tubes had been produced, droplets of the suspension of germinating spores were applied to areas on plate cultures of strain 56.6 where sclerotial bodies were abundant. Perithecia promptly matured in these areas. The same result was obtained when germinated ascospores from a mating of strain 56.6 (A) and strain 56.4 (B) were used. Ascospores which had been discharged against and caught upon the upper lid of a petri dish were washed into corn-meal decoction and heated in this at 60°C. for 40 minutes to stimulate germination. Presumably approximately 50% of the ascospores applied to the sclerotial bodies on the cultures of strain 56.6 were of the opposite reaction (B). Attempts to observe the germinated spores which had been placed on the culture were relatively unsuccessful. Ascospores could be more easily located than conidia because of their dark walls, but the germ tubes were usually lost in the maze of hyphae about them. In a few instances, however, the germ tubes could be followed; and it is interesting to note that some of them had more than doubled their original length in a period of twelve hours on the culture surface. While it is evident that their growth had been sharply checked, nevertheless at least some germ tubes apparently continued to elongate slowly.

In still another experiment fertilization was effected with mycelial mats. By making a heavy sowing of conidia of strain 56.4 in weak corn-meal decoction in a petri dish, a fine mat of hyphae was obtained which, so far as could be determined, produced no spores of any kind. Small squares of this mat were cut out with fine sterilized scissors and transferred to the surface of cultures of strain 56.6 bearing sclerotial bodies. Many of the sclerotial bodies in the areas to which the mycelial mats were applied enlarged and matured into normal perithecia.

RELATIONS OF TRICHOGYNES AND GERMINATED CONIDIA

Since germinated conidia can bring about fertilization as effectively and promptly as can ungerminated conidia, it seemed desirable to determine the details of the fertilization process. The same technique used earlier in connection with the study of trichogyne-conidium relations was employed. Preparations made *in toto* and stained with cotton blue showed that the receptive portions of a trichogyne upon coming in contact with a germ tube tend to wind about it in a spiral (Fig. 4). Cytoplasmic connections could not be observed, but evidence of gelatinization of trichogynous hyphae near the germ tubes fifteen hours after conidiation suggests that protoplasm of the complementary strain had entered. Frequently a single trichogyne system was found by its ramifications to have come in contact with several germinated conidia (Fig. 4), and more than one trichogyne branch was sometimes found in contact with a single germinated conidium.

FERTILIZATION EXPERIMENTS INVOLVING DEFINITE NUMBERS OF SPORES

Series of experiments were conducted which involved over a hundred plate cultures of strain 56.6 and in which was determined the exact number of spores—ungerminated or germinated—applied to marked areas on the plates.

In approximately 80% of the cases in which a droplet of sterile distilled water containing a single ungerminated conidium of strain 56.4 was placed on a spot at which sclerotial bodies were abundant, or on a spot covered by mycelial growth too young to have formed incipient perithecia, no ascocarps developed. In about 20% of the cases a single perithecium of unusual size matured. When several conidia were present in the droplet applied, a number of perithecia might be formed, but the number of perithecia rarely equaled the number of spores applied (Fig. 5, A–E). An analysis of the results obtained in many trials showed that on an average one perithecium was matured for every four or five conidia introduced.

A different picture appeared when germinated conidia were used. In these tests conidia of race 56.4 each with a germ tube no more than ten times the length of the original conidium were employed. In about 85% of the cases in each of which a single germinated spore was applied, a small

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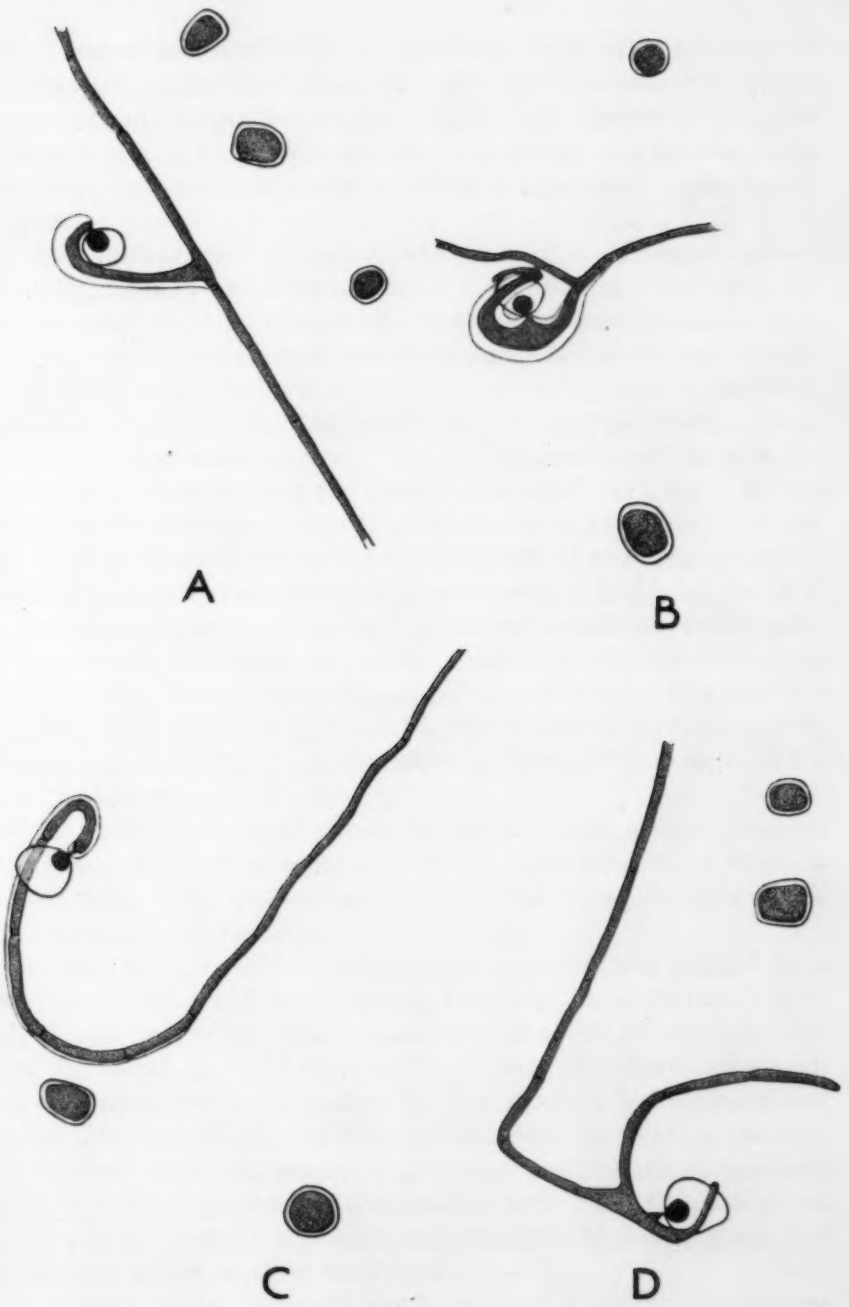
Explanation of Plate 3

Fig. 3. Detail of portions of trichogynous hyphae which have fused with conidia, 12 hours after conidiation. In each case the major part of the protoplasm of the attached conidium has passed into the trichogyne. Unattached conidia from the same fields are also shown. ×750.



BACKUS: NEUROSPORA FIG. 3

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cluster of ascocarps—usually 5 to 12—matured. In the other instances no perithecia at all appeared. If two or three germinated conidia in a droplet of water were introduced, frequently as many small clusters of ascocarps were formed (Fig. 5, F–G), although the result varied with the size of the droplet which in turn determined the chance of appreciable separation of the spores.

In these tests extreme precaution was taken to avoid contamination, particularly through the introduction of microconidia, since with the technique employed this seemed the most likely error. Controls were rigidly maintained, and these showed in general that the amount of error from the source mentioned was negligible. It is hardly possible, however, to carry out hundreds of faultless conidiations of this type. That occasionally a mistake was made is certain. The distribution of perithecia in the lower left large circle in the plate culture illustrated in Figure 5, G, was in disagreement with expectations from the results of many other cultures. In the circle in question, two well-defined patches of ascocarps appeared, although according to the records only one conidium had been placed in that area. It may be assumed that in this case two conidia had accidentally been introduced. The writer is confident, however, that relatively few accidents of this kind occurred. Checks indicate an error of less than 2% due to failures in determining accurately the number of conidia applied, and one of less than 5% due to difficulties involved in the transfer of the conidia to the surface of the culture.

When single germinated ascospores derived from a cross between strains 56.6 and 56.4 were applied to marked areas on cultures of strain 56.6, over 60% of the spots remained sterile; but when perithecia developed, they were usually several in a small cluster.

Likewise, when a single ungerminated conidium was applied in a marked area just beyond the advancing margin of the mycelium (Fig. 5, C–G), several perithecia—with a maximum of about 20—typically appeared. The development of these perithecia was not uniform, some perithecia appearing several days after the first sclerotia had enlarged and darkened (Fig. 5, C–E). If more than one conidium was placed in the location described, as a rule proportionally more fruiting bodies appeared (Fig. 5). In a few cases in which observations were made, the conidia had begun to germinate at the time when the advancing hyphae of strain 56.6 were about to obliterate them from view.

To account for the observed development of a cluster of ascocarps following the application of a single germinating spore of the complementary strain to the sclerotia-studded surface of a culture, two hypotheses may be suggested. One is that of a localized "diploidization." An-

other possibility is that while spore germination is ordinarily inhibited by products of mycelial metabolism, these products do not entirely stop growth of germ tubes already put forth. Some direct evidence in favor of this latter idea has been presented in a preceding section of this paper. A dwarf mycelium might develop under such conditions from a conidium; and trichogynes from various sclerotial bodies as they were reached by this slowly advancing mycelium would probably obtain nuclei of the complementary strain by effecting union with ordinary vegetative hyphae. To the writer the latter hypothesis seems the more reasonable. It also seems probable that the development of several ascocarps obtained when a single ungerminated conidium is placed just beyond the margin of mycelial growth, is to be explained in similar fashion.

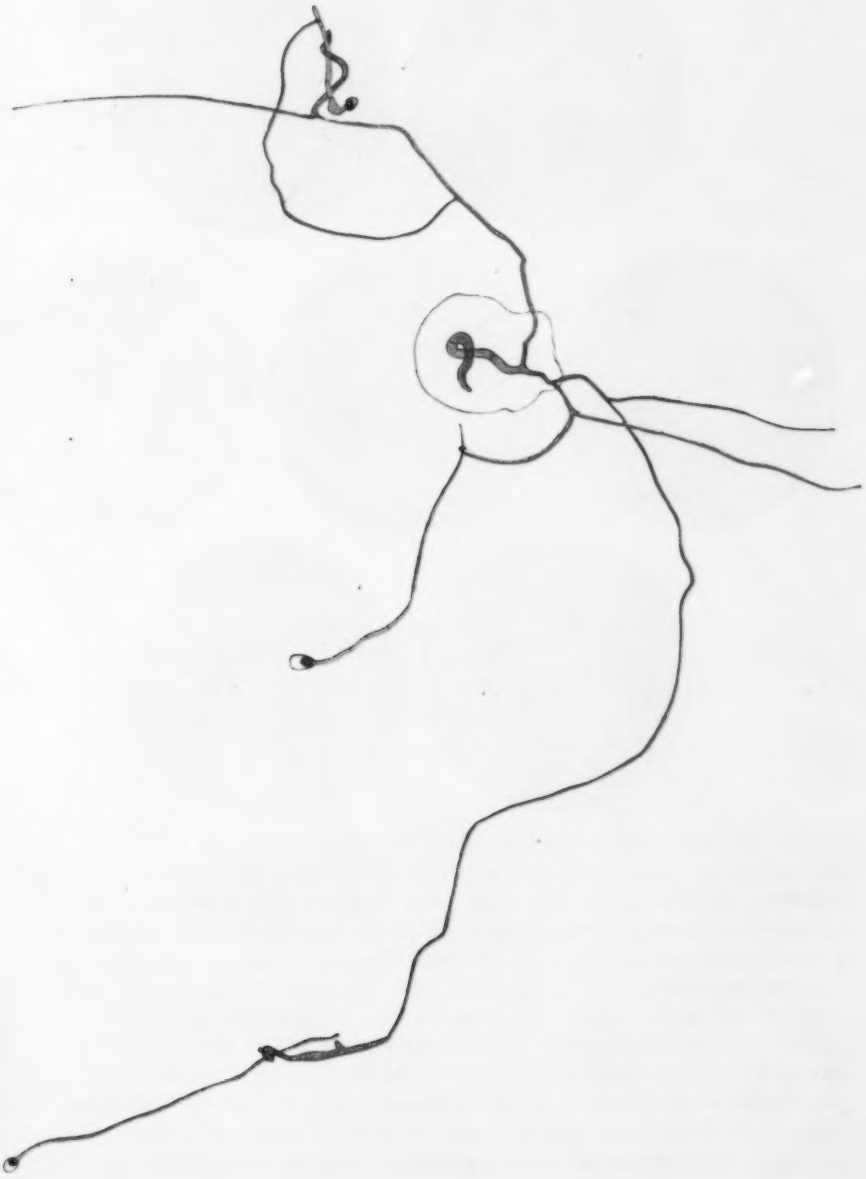
DISCUSSION

There has been given above an account of what happens when compatible conidia are placed in the vicinity of sclerotial bodies in cultures of *Neurospora sitophila*. It seems almost certain that when a detailed study of spermatial fertilization is undertaken, a picture very similar to what has been described in the case of conidial fertilization will be found. With the techniques employed in the present work a study of spermatial fertilization should present no great difficulties; and it seems very desirable that we should have the addition which such an investigation would contribute to our picture of the development of the perfect stage in this fungus. Despite the fact that in the case of a number of ascomycetes microconidia (spermatia) have now been shown to be functional bodies capable of effecting fertilization, no one has yet observed the actual fusion of these bodies with the trichogynes which have been shown to be present.

Experiments detailed in this paper have illustrated some of the various ways in which fertilization of sclerotial bodies of *N. sitophila* can be accomplished. That the transformation of sclerotial bodies into perithecia can be obtained by a variety of means was first shown by Dodge. In a paper published in 1935 (6) he refers to experiments—the details of which, however, are not given—which he says "indicate that young aerial hyphae and even trichogynes or trichogynous hyphae if they come in contact with trichogynous elements of the opposite sex reaction, are capable of effecting fertilization." It is evident that the thing of importance here is the introduction into the picture of cells of the complementary strain; and it is of

Explanation of Plate 4

Fig. 4. Relations of trichogyne system and germinated conidia, 9 hours after conidiation. ×175.



BACKUS: NEUROSPORA FIG. 4

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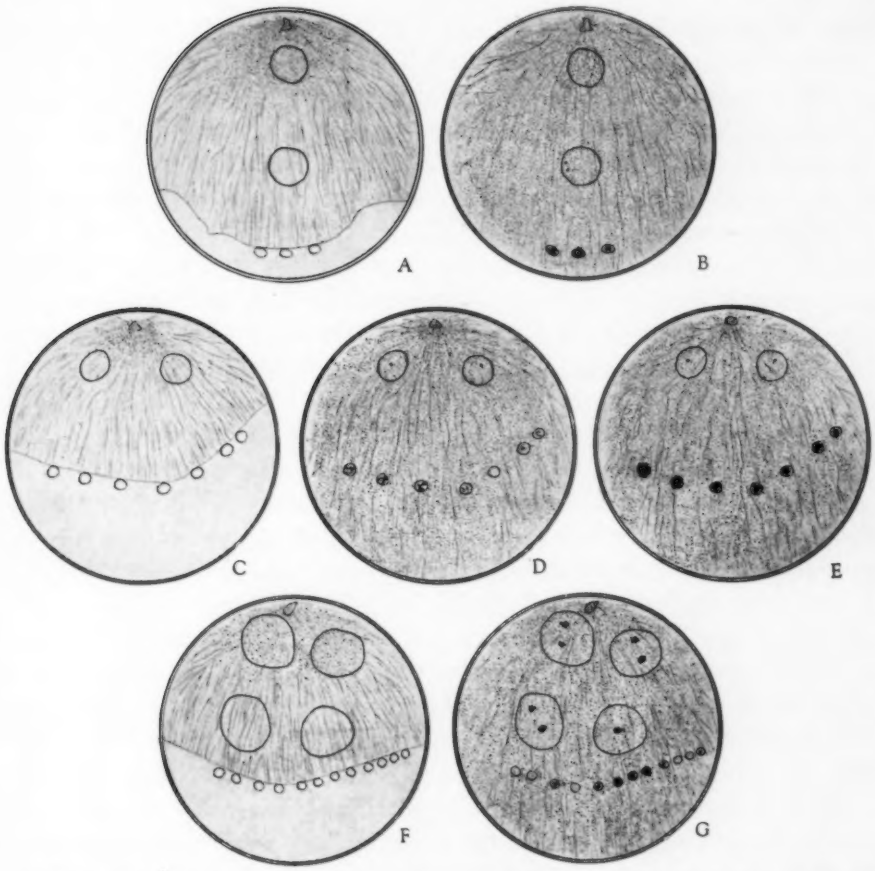

Fig. 5. A—Plate culture of *N. sitophila*, race 56.6 as it appeared at the time of conidiation (2 days after inoculation). Sclerotial bodies are abundant in upper large circle; no sclerotial bodies yet present in lower large circle. Ungerminated conidia of race 56.4 applied as follows: upper large circle—1 spore; lower large circle—9 spores; left small circle (just beyond margin of mycelium)—4 spores; center small circle—5 spores; right small circle—4 spores. B—The same plate 9 days after conidiation. 2 ascocarps in lower large circle; 20, 29, and 12 ascocarps in small circles, left to right. C—Plate culture of strain 56.6 at time of conidiation. Ungerminated conidia of strain 56.4 applied as follows: large circle at left—1 spore; large circle at right—3 spores; small circles, left to right, 6, 7, 5, 4, 4, 4, 1 respectively. D—The same plate 4 days later. E—The same plate 10 days later. F—Plate culture of strain 56.6 at time of conidiation. Sclerotial bodies abundant in the upper of the large circles, but absent in the lower two. To the large circles germinated conidia of race 56.4 applied as follows: upper left, 2 spores; upper right, 2 spores; lower left, 1 (?) spore; lower right, 1 spore. In the small circles just beyond the edge of the mycelium droplets from a suspension of ungerminated conidia applied. The droplets applied in succession to these circles, from left to right, were ascertained to be carrying spores as follows: no spores, no spores, 2 spores, no spores, 3 spores, 3 spores, 5 spores, 4 spores, 1 spore, no spores, no spores, 4 spores. G—Same plate 5 days later.

little importance in what form these cells are, provided their walls are not too thick (as in the case of ascospores). The present writer sees in this situation a remarkable case of plasticity and substitute sexuality—tendencies which are, however, by no means uncommon in ascomycetes. He is inclined to the view that the so-called microconidia are in reality male cells (spermatia) which, though still functional, are no longer essential to the development of the perfect stage. Dodge's (4, 5) observation that the microconidia of *Neurospora* may germinate supplies still further evidence of the plasticity of this fungus. If the conclusion is correct that the microconidia of *Neurospora* are male cells, then it follows that every race of *N. sitophila* may be considered hermaphroditic, since both male and female organs apparently may be formed on the same mycelium under suitable conditions. The performance of the sexual functions of the fungus appears to be regulated, however, by a superstructure of what may be termed compatibility factors which prevent self-fertilization. It is of course obvious that variability is favored by the compulsory interaction at every syngamy of two complementary strains.

N. tetrasperma Shear and Dodge (3, 11), a form with 4-spored asci, presents a peculiar situation in that one nucleus of each of the two compatibility groups is included in a single ascospore at the time of its formation. The mycelium which results when one of these ascospores germinates is essentially a mixo-chimaera. When ascogonia are formed they contain at the outset both kinds of nuclei; and ascocarps mature without the intervention of spermatia, conidia, or hyphae from any other mycelium. In fact it is reported (2) that no receptive hyphae are formed. Ordinarily, then, there is no occasion for spermatia to function in this form, or even scarcely any opportunity for them to do so. Yet these bodies are produced; and hence *N. tetrasperma* is hermaphroditic. Dodge (7) has designated this fungus as facultatively heterothallic since its ability to form perithecia on monosporous mycelia is due solely to the inclusion of two compatible nuclei in the same spore. Occasionally dwarf ascospores which contain only one nucleus at inception may be formed and these are not totipotent. They are either "A" or "B" in their reaction. An "A" thallus and a "B" thallus grown together in a petri dish react to produce perithecia. Dodge (5) has also shown that if monilioid conidia or spermatia from one strain are placed on marked areas of cultures of the opposite strain ascocarps will mature in these areas. It is thus clear that the spermatia of *N. tetrasperma* are not degenerate. One may suspect that the mechanism of fertilization in these cases where localized development of perithecia is obtained is probably the same as in *N. sitophila*. This seems all the more likely since Dodge (6) has found that the heterothallic races of *N. tetra-*

sperma form trichogynes. Dodge apparently did not study the situation in the normal races, but if Colson's conclusion that trichogynes are not formed in these is correct, it would seem, interestingly enough, that trichogynous outgrowths are produced in this species only when they can be of some service.

Gelasinospora tetrasperma Dowding is another facultatively heterothallic form, which is in many respects similar to *Neurospora tetrasperma* (10, 6, 8). In this species, however, neither spermatia nor conidia of any type have yet been discovered. It is possible that in the evolution of this fungus the spermatia, which became superfluous when the mixo-chimaera arrangement was developed, have completely disappeared from the picture. If so, all races of *G. tetrasperma* are essentially female; and when one mates heterothallic races, which may be obtained as in *Neurospora tetrasperma* (by germinating dwarf ascospores) and which fall into two compatibility groups, the bringing together of appropriate nuclei in the ascogonium is apparently accomplished through hyphal fusions and diploidization. Reduction seems to have proceeded further in *Gelasinospora* than in *Neurospora*, and neither the union of sexually differentiated protoplasts nor the range of substitute processes found in at least certain species of *Neurospora* is possible here.

SUMMARY

From a sclerotial body of *Neurospora sitophila* grows out a relatively complex branching trichogyne system originating from the apical region of the coiled ascogonium which lies in the interior of the sclerotial body. When a suspension of macroconidia of the complementary strain is placed on the surface of a culture bearing incipient perithecia, a union is effected between some of these conidia and various branches of the trichogyne system. The greater part of the protoplasm of the conidium enters the receptive trichogyne branch through a narrow cytoplasmic bridge.

Germinated conidia, germinated ascospores, and mats of mycelium of the proper strain also are capable of inducing the transformation of sclerotial bodies into perithecia. The details of the relations established between trichogynes and germinated conidia are described in the text.

Experiments are reported in which the number of ungerminated or germinated conidia applied to a given area was determined. On an average one perithecium is developed for every four or five ungerminated conidia placed on sclerotia-bearing regions of the culture. A single germinated conidium or ascospore similarly placed may, however, induce the development of a cluster of several ascocarps. A single ungerminated conidium placed just beyond the advancing margin of the mycelium frequently in-

duces likewise the development of a group of perithecia. A hypothesis is offered in explanation of these results.

The writer is grateful to Prof. E. M. Gilbert for counsel during the execution of this study. To Dr. B. O. Dodge and Prof. C. E. Allen he is indebted for helpful suggestions in the preparation of the manuscript.

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Additions to the Algae of Michigan*

CLARENCE E. TAFT

(WITH TWELVE FIGURES)

Previous to 1930 there had been no comprehensive survey of Michigan algae. A number of investigators had reported on isolated collections or localities, but none except Transeau (1917) had attempted to secure collections from widely separated areas. His work resulted in a list of 225 species, varieties, and forms, the largest single list published to that date.

Ackley (1932), following an extended survey of the state as well as a complete summary of the known literature on Michigan algae, published a list of 645 species, varieties, or forms of algae, exclusive of the Desmids and Diatoms, known to occur or reported as occurring in Michigan. During the same year (1932) Nichols and Ackley reported on the Michigan Desmids, listing 300 species, varieties, and forms for the state.

Since the appearance of these two papers in 1932 more than 100 additional records have been added by various workers.

The present list of 147 additional state records is the result of 155 collections made by the writer during the months of June, July, and August, 1936, while attending the summer session of the Michigan Biological Station, Douglas Lake, Michigan. Although a majority of the collections were made in the counties immediately surrounding the Station, some were secured in the Upper Peninsula, and a few in the western and southern parts of the state.

Of the 147 forms concerned in this report, there is one new species and one new variety, both in the genus *Oedogonium*. Of equal interest is the recording of several rare genera, a few of which have been figured.

With the exception of the county in which each species was collected, ecological data has been omitted.

To Dr. G. E. Nichols of the Department of Botany, Yale University, at whose suggestion the investigation was begun, I wish to express my sincerest appreciation for advice and aid during the collecting, and for certain determinations as acknowledged in the list of species, also to Dr. L. H. Tiffany of the Department of Botany, Northwestern University, and to Dr. E. N. Transeau of the Department of Botany, The Ohio State University, for criticism and advice concerning the Oedogoniaceae and the Zygnemales. For the correction of new records in the genus *Cosmarium* I am indebted to Dr. G. W. Prescott of the Department of Botany, Albion College. I am also indebted to the Michigan Biological Station for the

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use of collecting equipment, as well as to various staff members for information and transportation during the collecting.

The following are new species and varieties described in this paper:

Oedogonium minisporum Taft sp. nov.

Oedogonium oblongum Wittr. var. *minus* Taft var. nov.

SPECIES LIST

MYXOPHYCEAE

CHROOCOCCALES

APHANOCAPSA CASTAGNEI (De Bréb.) Rabenh. Cheboygan County.

EUCAPSIS ALPINA Clements and Shantz, Cheboygan, Presque Isle, Emmet and Otsego counties. This uncommon alga was found in a few of the bog lakes. The colonies were small and usually contained 8–32 cells.

GLOEOCAPSA RUPESTRIS Klebs, Otsego County.

GLOEOCHAETE WITTROCKIANA Lagerh. Cheboygan County. (Fig. 12). This interesting endophytic Myxophycean was found in two locations about three miles apart in Douglas Lake.

HOLOPEDIUM IRREGULARE Lagerh. Oakland County. (Figs. 10, 11). Previously reported only from the plankton of a North Dakota lake. The colony is a rectangular, broadly corrugate plate, $80\mu \times 250\mu$. Cells irregularly arranged, $2–3\mu$ in diameter.

MARSONIELLA ELEGANS Lemm. Emmet County. (Fig. 5).

RHABDODERMA LINEARE Schmidle and Lauterborn, Cheboygan County.

CHAMAESIPHONALES

PLEUROCAPSA MINOR Hansg. em. Geitler, Cheboygan County.

HORMOGONALES

ANABAENOPSIS ELENKINI V. V. Miller, Cheboygan County.

CALOTHRIX ADSCENDENS (Näg.) B. and F. Cheboygan County. This alga was identified by Dr. G. E. Nichols from collections made by the class in Freshwater Algae, University of Michigan Biological Station, 1936.

PLECTONEMA WOLLEI Farlow, Cheboygan County. Also identified by Nichols.

SPIRULINA LAXISSIMA G. S. West, Cheboygan County.

HETEROKONTAE

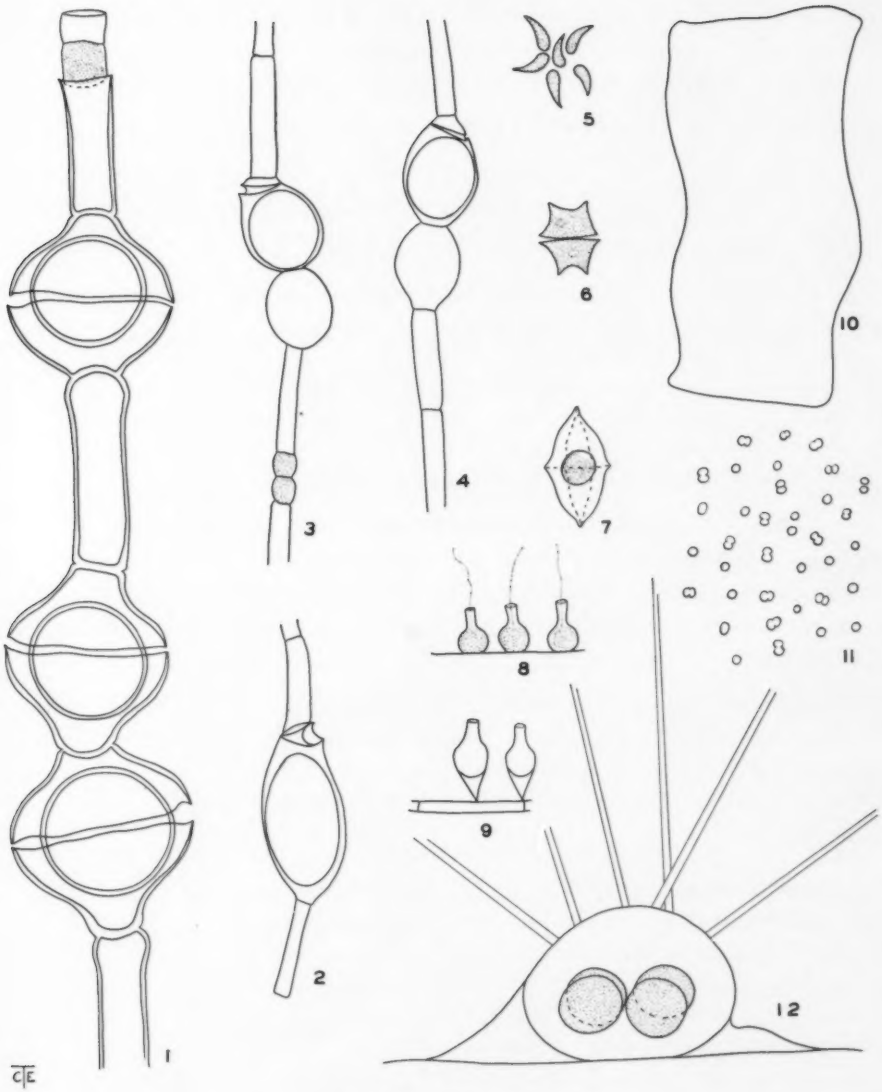
RHIZOCHLORIDALES

STIPITOCOCCUS URCEOLATUS W. & G. S. West, Grand Traverse County.

HETEROCOCCALES

CHARACIOPSIS LONGIPES (Rabenh.) Borzi, Macomb County.

OPHIOCYTIUM CAPITATUM var. LONGISPINUM (Mobius) Lemm. Cheboygan County.



Explanation of figures

Fig. 1. *Oedogonium minisporum* Taft sp. nov.
Figs. 2, 3, 4. *Oedogonium oblongum* Wittr. var. *minus* Taft var. nov.
Fig. 5. *Marsoniella elegans* Lemm.
Fig. 6. *Euastropsis richteri* (Schmidle) Lagerh.
Fig. 7. *Desmatractum bipyramidatum* (Chodat) Pascher.
Fig. 8. *Lagynion ampullaceum* (Stokes) Pascher.
Fig. 9. *Derepyxis dispar* (Stokes) Lemm.
Fig. 10. *Holopedium irregulare* Lagerh. Outline of colony.
Fig. 11. *Holopedium irregulare* Lagerh. Detail of cells.
Fig. 12. *Gloeochaete wittrockiana* Lagerh.

CHRYSOPHYCEAE

CHRYSOMONADALES

DEREPYXIS DISPAR (Stokes) Lemm. Macomb County. (Fig. 9).
MALLOMONAS CAUDATA Iwanoff, Cheboygan County.

RHIZOCHRYSIDALES

LAGYNION AMPULLACEUM (Stokes) Pascher, Cheboygan County. (Fig. 8).
RHIZOCHRYSIS LIMNETICA G. M. Smith, Cheboygan County.

CHRYSOCAPSALES

CHRYSOCAPSA PLANCTONICA (W. & G. S. West) Pascher, Cheboygan County.

CHLOROPHYCEAE

VOLVOCALES

GONIUM FORMOSUM Pascher, Cheboygan and Otsego counties.

TETRASPORALES

ELAKATOTHRIX GELATINOSA Wille, Cheboygan County.
ELAKATOTHRIX VIRIDIS (Snow) Printz, Cheboygan and Otsego counties.
GLOEOCYSTIS AMPLA Kuetz. Macomb, Cheboygan, Presque Isle, and Emmet counties.

ULOTRICHALES

MICROTHAMNION KUETZINGIANUM Näg. Cheboygan County.
RADIOFILUM CONJUNCTIVUM Schmidle, Cheboygan County.
URONEMA ELONGATUM Hodgetts, Cheboygan County.

OEDOGONIALES

BULBOCHAETE ANGULOSA Wittr. and Lundell, Cheboygan County.
BULBOCHAETE FURBERAE Collins, Macomb County.
BULBOCHAETE NANA Wittr. Cheboygan County.
BULBOCHAETE REPANDA Wittr. Cheboygan County.
OEDOGONIUM EXOCOSTATUM Tiffany, Cheboygan County.
Oedogonium minisporum Taft sp. nov. (Fig. 1).

Oe. monoicum, oogoniis singulis vel 2 continuis, subpyriform-globosis, raro subglobosis, operculo mediano apertis; oosporiis globosis, oogoniis non complentibus, membrana laevi; cellulis vegetativis capitellatis; antheridiis ?–2 sparis; cell. veget. 6–14μ×53–69μ; oogon. 30–42μ×34–42μ; oospor. 25–30μ×24–29μ; cell. antherid. 8–11μ×7–9μ.

Monecious; oogonia 1–2, subpyriform-globose, rarely subglobose, opening by a median operculum; oospore globose, rarely slightly subglobose, small, not filling the oogonium in either axis, color a pale yellow, wall smooth; vegetative cell capitellate; basal cell elongate; antheridia ?–2, sperms 2, division horizontal. Veg. cell 6–14μ×53–69μ; oogonium 30–42μ×34–42μ;

oospore 25–30μ×24–29μ; antheridium 8–11μ×7–9μ. Lake 16, Presque Isle County.

The combination of capitellate vegetative cells and small spores which do not fill the oogonium in either axis distinguishes this species from *Oed. psaegmatosporum* Nordst, which it superficially resembles in size and shape of the oogonium.

OEDOGONIUM MITRATUM Hirn, Macomb County.

Oedogonium oblongum Wittr. var. *minus* Taft var. nov. (Figs. 2, 3, 4).

Oogoniis singulis vel 3 continuis, oblongis, operculo apertis, circumscissone superiore vel supremo; oosporis ellipsoideis vel raro oboviformibus; cell. veg. 3–6μ×16–35μ; oogon. 13–16μ×20–23μ; oospor. 11–15μ×17–21μ; cell. antherid. 5–6μ×7μ. Oogonia 1–3, oblong, opening by a superior or sometimes supreme operculum; oospore ellipsoid, rarely obovoid, not quite filling the oogonium, color yellow-brown; suffultory cell sometimes enlarged. Veg. cell 3–6μ×16–35μ; oogonium 13–16μ×20–23μ; oospore 11–15μ×17–21μ; antheridium 5–6μ×7μ. Laizers Pond, Romeo. Macomb County.

This variety is separated from the species on the basis of size. In its dimensions it is approached by the variety *fusiforme* Jao, from which it differs in its smaller oogonia and oospores as well as the shape of the oogonium.

OEDOGONIUM AMBICEPS (Jao) Tiffany, Presque Isle County.

Veg. cell 9–12μ×30–40μ; oogonium 30–32μ×21–25μ; oospore 25μ×21μ; androsporangia 9–10μ×5–9μ.

Dimensions of the Michigan material have been given as they differ slightly from those given by Tiffany (1937).

OEDOGONIUM STELLATUM Wittr. Cheboygan County.

CHLOROCOCCALES

CHARACIUM ORNITHOCEPHALUM A. Braun, Cheboygan County.
CRUCIGENIA APICULATA (Lemm.) Schmidle, Otsego County.
CRUCIGENIA IRREGULARIS Wille, Otsego County.
CRUCIGENIA TETRAPEDIA (Kirchn.) W. & G. S. West, Cheboygan County.
CRUCIGENIA TRUNCATA G. M. Smith, Cheboygan County.
DESMATRACTUM BIPYRAMIDATUM (Chodat) Pascher, Macomb County. (Fig. 7).

This rare alga was collected in a sphagnum bog in which members of the class *Heterokontae* predominated.

Euastropsis richteri (Schmidle) Lagerh. Emmet County. (Fig. 6).

This alga, which has been previously reported from Wisconsin, was found in a small pool about three miles north of Pellston. The dimensions of the cells were well within the range given for this species, but as the figure shows, the apices of the cells are somewhat different, being broadly

retuse instead of notched. Smith, in his *Freshwater Algae of the United States*, says that it is possible to identify two-celled colonies of *Pediastrum* as *Euastropsis*. As *Pediastrum tetras* and *P. boryanum* were also in the collection, the writer hopes that further studies of Michigan algae will confirm this record.

FRANCEIA DROESCHERI (Lemm.) G. M. Smith, Emmet County.
GOLENKINIA RADIATA Chodat, Cheboygan County.
LAGERHEIMIA CILIATA (Lagerh.) Chodat, Cheboygan County.
LAGERHEIMIA CITRIFORMIS var. PAUCISPINA Tiffany and Ahlstrom, Cheboygan County.
PEDIASTRUM DUPLEX var. COHAERENS Bohlin, Macomb, Cheboygan, and Oceana counties.
PEDIASTRUM INTEGRUM forma GLABRA Raub. Emmet County.
QUADRIGULA CHODATI (Tanner-Fullman) G. M. Smith, Otsego County.
SELENASTRUM BIBRAIANUM Reinsch, Cheboygan County.
SCENEDESMUS ABUNDANS var. BREVICAUDA G. M. Smith, Emmet County.
SCENEDESMUS ACUTIFORMIS Schroeder, Macomb and Cheboygan counties.
SCENEDESMUS BRASILIENSIS Bohlin, Macomb and Otsego counties.
SCENEDESMUS PERFORATUS Lemm. Cheboygan County.
SCENEDESMUS QUADRICAUDA var. PARVUS G. M. Smith, Cheboygan County.
SCENEDESMUS QUADRICAUDA var. MAXIMUS W. & G. S. West, Cheboygan County.
SCENEDESMUS QUADRICAUDA var. WESTII G. M. Smith, Cheboygan County.
SCHROEDERIA JUDAYI G. M. Smith, Cheboygan County.
SORASTRUM AMERICANUM (Bohlin) Schmidle, Cheboygan and Otsego counties.
TETRAEDRON CAUDATUM (Corda) Hansg. Macomb, Presque Isle, Cheboygan, and Otsego counties.
TETRAEDRON CAUDATUM var. INCISUM Lagerh. Cheboygan County.
TETRAEDRON ENORME (Ralfs) Hansg. Cheboygan, Emmet, Otsego, and Manistee counties.
TETRAEDRON GIGAS var. GRANULATUM Boldt. Cheboygan County.
TETRAEDRON MINIMUM var. SCROBICULATA Lagerh. Cheboygan County.
TETRAEDRON TRIGONUM var. PAPILLIFERUM (Schroeder) Lemm. Cheboygan County.

ZYGNEMATALES

Zygnemataceae

MOUGEOTIA NUMMULOIDES (Hassall) DeToni, Emmet County.
MOUGEOTIA TENUIS (Cleve) Wittr. Cheboygan County.
SPIROGYRA ORIENTALIS W. & G. S. West, Cheboygan County.
ZYGNEMA CARINATUM Taft, Emmet County.
ZYGNEMA SYNADELPHUM Skuja, Cheboygan County.
ZYGNEMOPSIS MINUTUM Randhawa, Cheboygan and Emmet counties.

Mesotaeniaceae

CYLINDROCYSTIS BREBISSONII Menegh. Cheboygan County.
CYLINDROCYSTIS BREBISSONII var. MINOR W. & G. S. West, Presque Isle County.
GONATOZYGON BREBISSONII DeBary, Cheboygan County.
GONATOZYGON BREBISSONII var. MINUTUM W. & G. S. West, Cheboygan County.
GONATOZYGON KINAHANI (Arch.) Rabenh. Cheboygan County.
GONATOZYGON LEIODERMUM Turner, Cheboygan County.
GONATOZYGON PILOSUM Wolle, Cheboygan and Emmet counties.
MESOTAENIUM DE GREYI var. BREVE West, Cheboygan County.
NETRIUM DIGITUS var. LAMELLOSUM (DeBréb.) Grönblad, Cheboygan County.

Desmidiaceae

ARTHRODESMUS BULHEIMII var. SUBINCUS W. & G. S. West, Cheboygan County.
ARTHRODESMUS PHIMUS Turner, Cheboygan County.
ARTHRODESMUS PHIMUS var. OCCIDENTALIS W. & G. S. West, Cheboygan County.
ARTHRODESMUS TRIANGULARIS var. INFLATUS W. & G. S. West, Cheboygan County.
CLOSTERIUM ABRUPTUM West, Presque Isle County.
CLOSTERIUM ACICULARE var. SUBPRONUM W. & G. S. West, Presque Isle County.
COSMARIUM DECORATUM W. & G. S. West, Cheboygan County.
COSMARIUM DEPRESSUM var. RENIFORME W. & G. S. West, Cheboygan County.
COSMARIUM GLOBOSUM forma MINOR Boldt. Cheboygan County.
COSMARIUM HUMILE var. STRIATUM (Boldt.) Schmidle, Cheboygan County.
COSMARIUM ISTHMIUM West, Cheboygan County.
COSMARIUM NASUTUM Nordst. Cheboygan County.
COSMARIUM OBSOLETUM (Hantzsch) Reinsch, Cheboygan County.
COSMARIUM PSEUDOCONNATUM Nordst. Cheboygan County.
COSMARIUM QUADRUM Lund. Emmet County.
COSMARIUM REPANDUM forma MINOR W. & G. S. West, Cheboygan County.
COSMARIUM TINCTUM Ralfs. Cheboygan County.
DESMIDIUM COARCTATUM Nordst. Cheboygan County.
DESMIDIUM SWARTZII var. QUADRANGULATUM (Ralfs) Roy, Cheboygan and Presque Isle counties.
DOCIDIUM BACULUM DeBréb. Cheboygan County.
DOCIDIUM UNDULATUM Bailey, Cheboygan County.
EUASTRUM BINALE forma HIANS West, Cheboygan County.
EUASTRUM PECTINATUM var. BRACHYLOBUM Wittr. Cheboygan County.
EUASTRUM PULCHELLUM DeBréb. Cheboygan County.

EUASTRUM SINUOSUM var. REDUCTUM W. & G. S. West, Crawford County.
EUASTRUM VENTRICOSUM Lund. Cheboygan County.
MICRASTERIAS APICULATA var. FIMBRIATA forma SPINOSA Bissett, Cheboygan County.
MICRASTERIAS CONFERTA var. HAMATA Wolle, Cheboygan County.
MICRASTERIAS CONFERTA var. NOVAE-TERRAE Cushman, Cheboygan County.
MICRASTERIAS EXPANSA Bailey, Cheboygan County.
MICRASTERIAS MURICATA (Bail.) Ralfs, Presque Isle County.
MICRASTERIAS RADIATA var. GRACILLIMA G. M. Smith, Presque Isle County.
MICRASTERIAS SOL var. ORNATA Nordst. Cheboygan County.
PENIUM CUCURBITINUM forma MINOR W. & G. S. West, Cheboygan County.
PENIUM EXIGUUM West, Cheboygan County.
PENIUM MINUTUM (Ralfs) Cleve, Cheboygan and Presque Isle counties.
SPHAEROZOSMA EXCAVATUM var. SUBQUADRATUM W. & G. S. West, Cheboygan County.
STAURASTRUM CONTORTUM G. M. Smith, Cheboygan County.
STAURASTRUM CURVATUM W. West, Cheboygan County.
STAURASTRUM CUSPIDATUM var. CANADENSE G. M. Smith, Cheboygan County.
STAURASTRUM CUSPIDATUM var. CORNULATUM Gutw. Cheboygan County.
STAURASTRUM LONGISPINUM (Bail.) Archer, Cheboygan County.
STAURASTRUM LONGISPINUM var. BIDENTATUM (Wittr.) W. & G. S. West, Cheboygan County.
STAURASTRUM MEGACANTHUM var. SCOTICUM W. & G. S. West, Cheboygan County.
STAURASTRUM OPHIURA Lund. Cheboygan and Otsego counties.
STAURASTRUM PARADOXUM var. LONGIPES Nordst. Cheboygan County.
STAURASTRUM PENTACERUM (Wolle) G. M. Smith, Cheboygan County.
STAURASTRUM ROTULA Nordst. Cheboygan County.
STAURASTRUM SUBLAEVISPINUM W. & G. S. West, Cheboygan County.
TETMEMORUS BREBISSONII (Menegh.) Ralfs, Presque Isle County.
TETMEMORUS GRANULATUS (DeBréb.) Ralfs, Presque Isle, Crawford and Chippewa counties.
TETMEMORUS GRANULATUS var. ATTENUATUS West, Cheboygan County.
XANTHIDIUM ARMATUM var. FISSUM Nordst. Cheboygan County.
XANTHIDIUM ARMATUM var. IRREGULARIUS W. & G. S. West, Cheboygan County.
XANTHIDIUM CRISTATUM var. UNCINATUM DeBréb. Macomb, Cheboygan, Presque Isle, and Otsego counties.
XANTHIDIUM TORREYI Wolle, Cheboygan County.

DINOPHYCEAE

GYMNODINIUM PALUSTRE Schilling, Cheboygan County.

PERIDINIUM PUSILLUM (Penard) Lemm. Emmet County.
PERIDINIUM WILLEI Huitfeld-Kass, Cheboygan County.

EUGLENOPHYCEAE

PHACUS ACUMINATUS Stokes, Cheboygan County.
PHACUS PYRUM (Ehr.) Walton, Cheboygan and Otsego counties.
TRACHELOMONAS HISPIDA (Perty) Stein, Cheboygan and Emmet counties.
TRACHELOMONAS HISPIDA var. CORONATA Lemm. Oceana County.
TRACHELOMONAS HISPIDA var. PUNCTULATUM Skvortzow, Oceana County.
TRACHELOMONAS VOLVOCINA Ehrenb. Oceana County.

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The Cause of Pecky Cypress

WILLIAM A. MURRILL

(WITH SIX FIGURES)

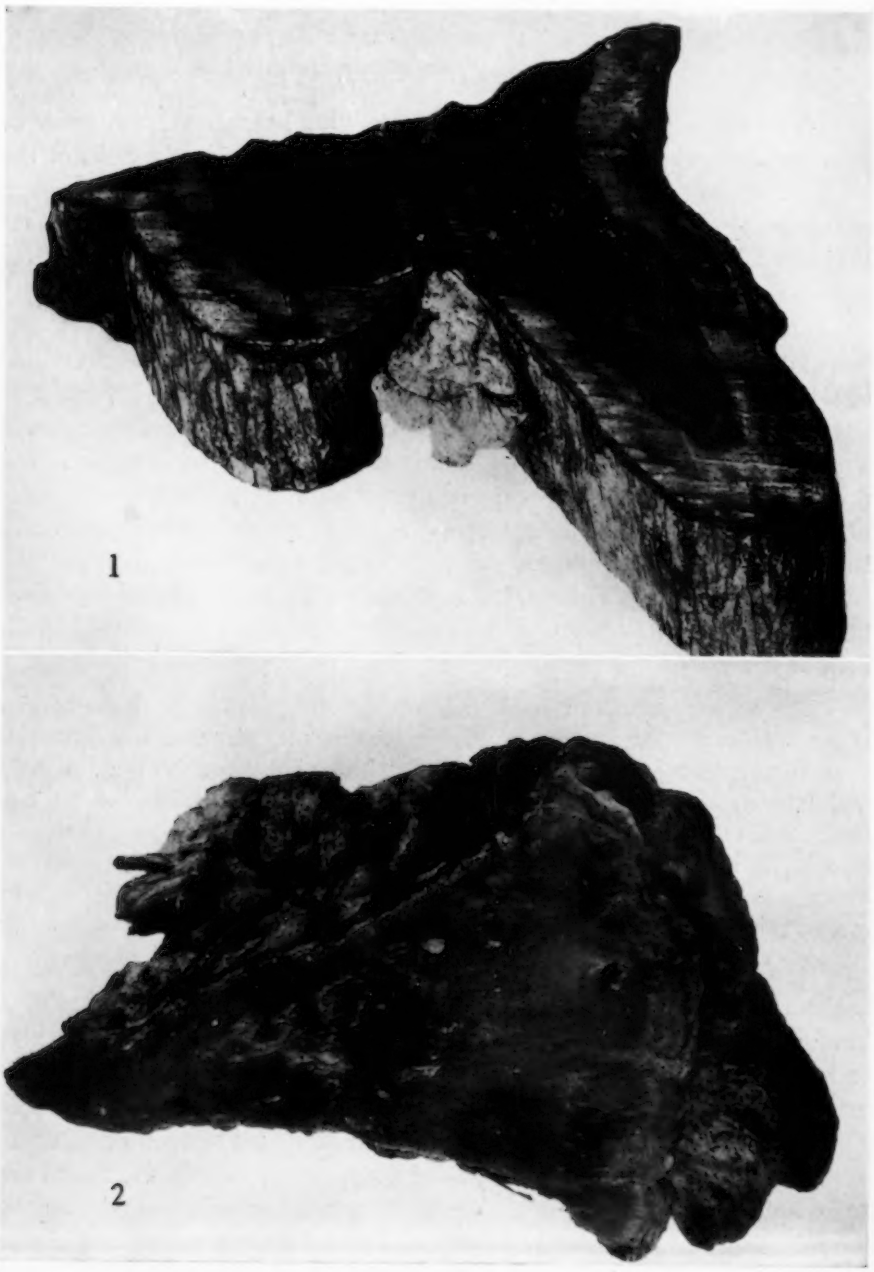
There was a time when "pecky cypress" lumber was thrown away or made to serve the lowliest purposes but now it shines in the halls of the mighty. For antiques and interior finishing it has few equals. It was even suggested to me recently that trees might have to be inoculated to meet the increasing demand. At present, only about ten per cent of our cypress trees show "peckiness."

The cause of "peckiness" is said to be the mycelium of a bracket fungus belonging to the genus *Fomes* in the Polyporaceae. It was first described by M. C. Cooke from British Guiana in 1884 (Grevillea **13**: 119) and was later found in other parts of tropical America and also in the southern United States. The name *Fomes geotropus* was selected for it because the dried brackets are noticeably curved downward. *F. Auberianus* (Mont.) Murrill, a species confined to tropical America, resembles it in form and habit but is much thinner and conspicuously zonate. *Fomes ulmarius* Fr., which attacks elms in Europe, is a still closer relative. The following scientific description of *F. geotropus* was used by the author in one of his publications:

Pileus woody, conchate, 6–12×10–20×2–4 cm.; surface pruinose to glabrous, rugose, anoderm, azonate, irregularly concentrically undulate, stramineous to cremeous; margin tumid, pallid, brownish when bruised, slightly undulate, deflexed; context corky to woody, pallid to isabelline, 0.5–1.5 cm. thick; tubes distinctly stratified, 0.5–1.5 cm. long each season, pale chestnut-colored, fading out in the older layers, mouths circular, 5 to a mm., edges thin, entire, rose-colored when fresh, becoming darker and discolored with age or when bruised; spores globose or subglobose, smooth, hyaline, granular, 5–7μ; cystidia none.

The Ellis Collection at the New York Botanical Garden contains a number of fine specimens of this fungus collected by Calkins and others on hardwood trunks in the Gulf States. Since coming to Florida I have collected it on box elder and magnolia, and the herbarium here also contains specimens found on sweet gum, linden, red bay, and winged elm. These were all taken from decayed trunks of living trees, usually near the base or in hollows, and infection doubtless occurred through wounds. About the middle of last August, Mr. West and I found some brackets on the side of an immense dead magnolia trunk which had been so weakened that it had blown over in a storm several years ago.

Johnson and Edgerton in their report upon *Fomes geotropus* on *Mag-*



1. *Fomes geotropus* on bald cypress $\times\frac{1}{4}$. The hymenophore has developed between two buttresses near the base of the diseased trunk.

2. *Fomes geotropus* $\times 1$. This shows the under side of the hymenophore figured in Figure 1, which is six years old.

3. Stump of the tree hollowed out by the mycelium. In the foreground are the two buttresses between which the hymenophore appeared.

4. The cypress trunk cut into sections to trace the progress of the decay. The author is showing the position of the bracket, while next beyond him are Messrs. Voorhees and Rhoads, with Mr. West in the background taking notes.

5. Termination of the decay shown at the center of two adjacent sections of the trunk.

6. *Fomes geotropus* on a dead magnolia log. The mass is about a foot high and six inches wide, the upper surface old and discolored, the hymenium fresh and cream-colored. Photo by Dr. R. P. Wodehouse.

nolia grandiflora in Louisiana (Mycologia **28:** 293. 1936) make no mention of finding the brackets on the dead fallen logs but only near the base of diseased living trunks. Mr. W. H. Long (Phytopathology **4:** 39. 1914) states that he found the hymenophores on magnolia and also upon tupelo gum, black gum, sweet gum, elm, and maple among the hardwoods, as well as upon bald cypress.

The occurrence of the brackets upon cypress trunks seems to be rare, otherwise they would have been more frequently found. On July 27, 1938, Mr. West and I were exploring a hammock south of Newnan's Lake, a few miles from Gainesville, when we stumbled upon a tree of *Taxodium distichum* bearing a bracket of what appeared to be *Fomes geotropus* upon its trunk three feet above the ground. It had grown out between two buttresses and proved to be six years old. Mr. Adolph Vidal, the owner of the land, kindly gave us permission to cut the tree, which we did on August 25, 1938.

Assisting us in the investigation of the rot in this particular tree were Dr. G. F. Weber, Plant Pathologist in the Florida Agricultural Experiment Station, Mr. R. K. Voorhees, Assistant Plant Pathologist, and Dr. A. S. Rhoads, Plant Pathologist at Cocoa, Florida. The photographs were taken by Dr. Weber and all the records were made by Mr. Erdman West, Mycologist in the Florida Agricultural Experiment Station.

As the illustrations will show, sections were made of the trunk at various points and the decay traced from the hollow base upward along the trunk to its termination in sound wood. The fungus probably entered the trunk at a wound or burn near its base, and, after years of growth, the bracket probably emerged at or near the same point. When infection takes place at a broken branch some distance above ground, the mycelium probably travels both upward and downward in the trunk and brackets are formed wherever there are openings to the light. If the branch stub does not heal over, this would be a very likely place to look for a bracket.

In a pamphlet recently sent me by the Southern Cypress Manufacturers Association, with offices at Jacksonville, the following description of the decay in bald cypress is given:

"The fungus invades the trunk of the tree, which it honey-combs in varying degrees, leaving pockets in the wood from a quarter of an inch to an inch in diameter and often several inches long. These pockets are filled with a brown powder, a deposit from the fungus, antiseptic in action, which in time apparently arrests the further progress of the fungus itself. Another peculiarity of this fungus is that it stops working as soon as the tree is felled and never again attacks wood sawn from these infected trees."

The appearance and effects of this rot in cypress have long been known.

The self-toxicity of the mycelium, however, might be open to discussion; and why the fungus ceases to grow in cypress when it is cut and develops brackets on a magnolia log years after the trunk is dead is another question not so easily answered. It may be that careful cultures and inoculations will help to solve these questions as well as certain other puzzles connected with this very interesting fungus. But, as the young doctor said to himself while scattering bottles on a lonely curve, in this business one must have patience.

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Barbula in North America north of Mexico[1]

WILLIAM CAMPBELL STEERE

Hedwig, in his classic "Species Muscorum" (1801), described as new five species of *Barbula*, *B. acuminata*, *B. agraria*, *B. apiculata*, *B. lanceolata*, and *B. stricta*, from American specimens. Since the appearance of Hedwig's publication, more than sixty other species of *Barbula* have been described as new or reported to occur in North America north of Mexico, not counting the twenty-odd species of *Barbula* which are really members of the genus *Tortula*.

Most of the species were described by various European bryologists, of necessity unfamiliar with the great range of variation of each species in the field. The original descriptions appeared in a multitude of scientific journals, reports of expeditions and other publications, many of them abroad. As a result of the scattering of descriptions and specimens for comparison, it apparently became progressively easier for authors to describe more new species than to identify the old ones.

Perhaps, also, a false diagnostic value was placed upon extremely variable characteristics in an extremely variable group of species. Nearly every diagnostic character used in *Barbula* varies within rather wide limits and most species are best identified by a complex of characteristics rather than by any single one. This situation is especially well discussed by Hilpert (1933) whose interesting researches demonstrate the very slight amount of taxonomic significance to be derived from such characteristics as, for example, the presence of a central strand in the stem, the shape of the stem in cross section, and the size of the annulus. This last structure, given a good deal of taxonomic importance by earlier bryologists, is shown to be completely valueless as a diagnostic feature by Hilpert, the only valid distinction being between the persistent and the revoluble annulus.

The choice of single, very variable characteristics to separate species, by earlier authors, often lead to their confusion. For instance, Lesquereux (1865) maintained *Barbula flexifolia* Hampe as a valid species, comparing it to *B. vinealis* Brid., as follows: "The characters separating this species from *Barbula vinealis* are, 1st, The leaves crisped when dry, squarrose-reflexed when humected, with revolute margins. 2d, The somewhat narrower, dark red capsule, with a longer operculum. 3d, The longer and more twisted teeth of the peristome, and their red color. These last characters are unreliable, the teeth varying in color, and being more or less twisted even on the same specimen, according to the age of the capsule. The char-

[1] Papers from the Department of Botany and the Herbarium of the University of Michigan, No. 674.

acters taken from the leaves are also unreliable." The differences between *B. cylindrica* (Tayl.) Schimp. and *B. vinealis* Brid. are still puzzling, of course, but we may now use a large series or complex of quantitative criteria and thus separate two closely related species on a more or less statistical basis.

One usage of the earlier authors seems to me clearly to violate an important biological principle. In general, little evidence supports the expectation that several closely related species of the same genus can maintain themselves as separate and independent species if they occupy exactly the same habitats and geographic ranges. In fact, each species seems to occupy a small niche in the environment in which it does not compete to any extent with other species in the same genus, certainly not those which are closely related. If two species have exactly the same habitat, ordinarily they have different geographic ranges, or are not at all close phylogenetically. Consequently, when an author manages to identify three or four species of the same genus, of which perhaps one is proposed as a new species, from the very same tuft, there seems good reason to suspect that he is confusing habitat or genetic variability with his species concept.

No real effort has ever been made to clear away the confusion which surrounds almost every one of our American species of *Barbula*, probably because of the labor involved and also because of the large number of genera which are in exactly the same condition, for the same reasons. The only survey of the American species of the genus *Barbula* is that in Lesquereux and James' "Manual," published in 1884. Insofar as *Barbula* is concerned, at least, the treatment was essentially a compilation. Although a few comments were made concerning the presumptive identity of two or more "species," no critical attempt was made to settle definitely any of these problems. In the more than a half-century since the "Manual" appeared, critical notes on a few species have been published and several conscientious bryologists have indicated their opinions as to probable synonymy in herbarium notes. It is more than likely that the large number of new species proposed by N. C. Kindberg, alone or in collaboration with C. Müller, has been responsible in large part for the delay in any attempt to revise the American species of *Barbula*.

During the past two years, which have been spent in the revision of the genus *Barbula* for Dr. A. J. Grout's "Moss Flora of North America, north of Mexico" (Steere, 1938b), I have had occasion to see the type material of nearly every one of the species of *Barbula* originally described from our range, thanks to the kindness of many individuals and institutions. It has been found possible to reduce the great assemblage of species of *Barbula* to a tentative order, and to identify the majority of the species more

recently proposed as new with older and better established species.

Since many of the reductions of names to synonymy and recommendations for the summary discard of others are perhaps open to criticism, I am taking this opportunity to present my reasons for the disposition of each name. As such a series of critical notes, especially when its bearing is largely upon nomenclature and taxonomic status, is of no particular importance in identification, and so is beyond the scope of a manual, most of the comments which follow serve to supplement but not duplicate those which have already appeared in the revision of *Barbula*. It is hoped that the disposition of many specific names which have not appeared in the literature for several decades, but which still exist as puzzles in every herbarium, may be of some use to those beset by such puzzles.

In the following list of species, I have almost completely ignored the new varieties which Kindberg proposed because quite uniformly they do not even belong to the species to which he assigned them. Also nearly every variety has a very involved history, as for example his "*Barbula gracilis* var. *squarrulosa*" which he later cited as a synonym of his new species "*Barbula subicmadophila*," which in turn is actually a synonym of *B. rubiginosa* Mitt., with no relationship whatsoever to either *B. gracilis* or *B. icmadophila!* After a few experiences of this sort, I did not go to the trouble of identifying the remainder of Kindberg's "new" varieties, and should recommend that they be totally disregarded, at least in *Barbula*.

The following species of *Barbula*, which have been described as new from specimens collected in our range, no longer fit our concept of the genus *Barbula*, as a result of the drawing of narrower generic lines, and for the most part belong to *Tortula: B. astoriensis* Broth., *B. Bolanderi* Lesq., *B. brachyangia* C. Müll. & Kindb., *B. brachypoda* Card. & Thér., *B. brevipes* Lesq., *B. carnifolia* C. Müll. & Kindb., *B. Egelingi* Schlieph., *B. laeviuscula* Kindb., *B. latoexcisa* C. Müll. & Kindb., *B. leptotricha* C. Müll. & Kindb., *B. macrotricha* Card. & Thér., *B. megalocarpa* Kindb., *B. papillinervis* C. Müll. & Kindb., *B. pseudoaciphylla* Kindb., *B. rotundoemarginata* C. Müll. & Kindb., *B. rufipila* Card. & Thér., *B. subcarnifolia* C. Müll. & Kindb., *B. subcuneifolia* Kindb., *B. submegalocarpa* Kindb.

Species of Barbula Described or Reported from North America[2]

1. *Barbula acuminata* Hedw., Sp. Musc. **117.** 1801.

Hedwig himself appended to his diagnosis of the species the remark "An haec eadem, quae mea barbula *unguiculata?*" and Schwaegrichen

[2] Valid names are written in capital letters, those reduced to synonymy in italics.

later affirmed this query. Cardot (1899), however, as the result of his study of the type material and Hedwig's illustrations, considered it a synonym of *B. fallax* Hedw., and is followed by Paris (1904). This name, based on a specimen from Lancaster, Pennsylvania, was either neglected and forgotten, or else misused, yet occasional specimens bearing it are still encountered. Although I have not seen the type specimen, I am convinced, from Cardot's words, that it is *B. fallax*.

2. BARBULA ACTUA (Brid.) Brid., Method. Musc. **96.** 1822.
Tortula acuta Brid., Musc. Recent. Suppl. **1:** 265. 1806.
Barbula gracilis Schwaegr., Sp. Musc. Suppl. **1**[1]**:** 125. 1811.

This species, which seems usually to pass under the name of *B. gracilis* in the American literature, has been reported from a number of widely separated localities. Its greatest abundance or most general occurrence seems to be in British Columbia, Idaho, Montana, New Mexico, Arizona and California, yet there are a few specimens from scattered stations in the eastern United States, from New England southward, in the mountains. The specimens are all rather perplexing, however, for very few of them agree really well with European material, all being slightly papillose and differing in other more subtle and indefinable ways. What adds still more difficulty to the problem of identifying the so-called American *B. acuta* is that the eastern and western specimens do not agree well. This fact, in view of the great variability of the material, which apparently fruits only very rarely, and the very curious geographical distribution of the supposed species in our range, arouses the suspicion that we may be dealing here with a complex of two species, one or both of which may be different from the European *B. acuta*.

3. BARBULA AGRARIA Hedw., Sp. Musc. **116.** 1801.
Tortula agraria Sw., Fl. Ind. Occ. **3:** 1763. 1806.
Barbula Raui Aust., Bull. Torrey Bot. Club **6:** 43. 1875.

This species, which was described from Jamaica and Santo Domingo, and is widespread through tropical and subtropical America, has been placed about equally often in *Barbula* and *Tortula* by various authors. In the structure of the costa, in cross-section, the relationship is evidently to *Barbula*. The shape of the leaf, on the contrary, is typically that of *Tortula*, in which the leaf becomes wider above a narrow base. The leaf margins are plane when moist and somewhat involute when dry, neither condition characteristic of *Barbula*. The peristome, however, is aberrant for either genus, and there are perhaps sufficient differences otherwise to justify eventually the erection of a new genus. For *B. agraria* and related species, Müller (1849) erected the section *Hyophiladelphus*. Brotherus

(1924) recognized this section, but restricted it to include only *B. agraria* and several too closely related species. Those from the West Indies and Central America will eventually turn out to be conspecific, no doubt.

4. *Barbula amplexa* Lesq., Trans Amer. Phil. Soc. **13:** 5. 1865.

The original description of this species very clearly indicates the genus *Tortula*, and Lesquereux compared it somewhat indirectly to *T. marginata* (Bry. eur.) Spruce. In spite of this authoritative evidence that the species should be transferred to *Tortula*, it has been widely distributed in relatively recent exsiccati as *B. amplexa*, *No. 180* in Holzinger's "Musci Acrocarpi Boreali-Americani," for example. Furthermore, Brotherus, in the second edition of Engler und Prantl (1924, p. 280) retained it in *Barbula*, and, on the basis of the sheathing perichaetial leaves, placed it in the section *Streblotrichum*. I have examined the type material, however, and can substantiate, without question, Lesquereux's implication that the species is a member of the genus *Tortula*, although it cannot be safely said yet whether or not it is a valid species in *Tortula*.

5. *Barbula andreaeoides* Kindb., Rev. Bryol. **32:** 36. 1905.

This remarkable little moss with obtuse, cochleariform leaves is obviously no *Barbula* at all, but a form of *Andreaea Rothii* Web. & Mohr. I am grateful to Dr. A. J. Sharp for confirming my disposition of this "species."

6. *Barbula apiculata* Hedw., Sp. Musc. **117.** 1801.

This species is based on a specimen which came, insofar as the original description informs us, from "Pensilvania." According to Cardot (1899), the type specimen, which he has examined, bears on its label the notation that it was collected at Lancaster. He also concluded that the type material represents the form of *B. unguiculata* Hedw. called var. *apiculata* in the Bryologia Europaea.

7. *Barbula artocarpa* Lesq., Trans. Amer. Phil. Soc. **13:** 4. 1865.

Lesquereux says of this: "Except for its pretty large annulus, this species would agree with *Barbula gracilis* Schw., which it exactly resembles by the ramification, the form of the leaves and of the capsule." I have seen the type specimens, from Mount del Diablo, California, and find that the leaf cells are rather distinctly papillose, and that several characteristics preclude any relationship to *B. acuta*. In fact, from the widely spreading leaves, the strongly recurved leaf margins, the costa ending in the leaf apex and the pale, dusty red peristome, the only possible conclusion is that *B. artocarpa* is only a small form of *B. vinealis* Brid., and must become a synonym of it.

8. *Barbula Bakeri* Card. & Thér., Bot. Gaz. **37**: 367. 1904.

The problem as to the use or disposal of this name is very difficult to settle satisfactorily. Several different collections, each from a different station, were issued as "*Barbula Bakeri* Card. & Thér. n. sp." Furthermore, all these not too similar specimens are cited in the original description, with no indication as to which one should be considered the type. The problem is made still more perplexing by the fact that at least two different species are represented in the collections. In a comment supplementary to the original description, and published also on the label of both Baker's "Pacific Slope Bryophytes" *No. 33*, and Holzinger's "Musci Acrocarpi Boreali-Americani" *No. 157* (=Baker's "Pacific Slope Bryophytes" *No. 351*), the authors say: "A species belonging to the perplexing group of B. fallax Hedw., differing from this species by its smooth or very slightly papillose leaves with margins more broadly revolute, and by its shorter, slightly twisted peristome."

As shown elsewhere, *B. fallax* Hedw. is out of the question anyhow, since it apparently does not occur west of the Rocky Mountains. All the specimens issued as *B. Bakeri* have short cells on the ventral surface of the costa, which still further eliminates any possibility of a relationship to *B. fallax*. The original description suggests a member of the *B. vinealis* group, which is substantiated by an examination of the original material. Baker's *No. 33*, mentioned above, collected at "Stanford University, Santa Clara County, California, October 26, 1901; common in small mats on stones bordering flower beds" is fairly typical *B. vinealis*. Baker's "Pacific Slope Bryophytes" *No. 352*, from "Foothills near Stanford University, Santa Clara County, California, March 22, 1902" is a smaller plant with a much shorter seta. Baker's *No. 351*, collected at "Alma, Santa Clara County, California, March 23, 1902; on a boulder" was issued, still with Baker's label, by Holzinger as *No. 157* in his "Musci Acrocarpi Boreali-Americani" with the comment: "Type station, Stanford University." Baker's *351* and *352* are rather similar, but differ from *B. vinealis* in the more uniform areolation and the leaves being rather strongly revolute from base nearly to apex. From these characteristics, as well as the short, only slightly twisted peristome, a form of *B. brachyphylla* Sulliv. with rather more acute leaves than usual, seems to be indicated.

9. *Barbula Beecheyi* Lesq. in Watson, Bot. Calif. **2**: 372. 1880.

According to Lesquereux and James (1884) this is a synonym of *B. cylindrica* (Tayl.) Schimp.

10. Barbula Bescherellei Sauerb. in Jaeg., Adumb. **2**: 673. 1878. *B. rigidula* Besch., Prodr. Bryol. Mex. **36**. 1871, not *B. rigidula* (Hedw.) Milde.

Mr. Bartram has recognized this Mexican species in our range, from both Arizona and New Mexico. Concerning its distribution in Arizona, he says (1927): "It is abundant in the oak forests of the Patagonia and Santa Rita Mts., and frequently grows in dense cushions around the bases of the trees. The species is ordinarily sterile in Arizona but a fertile colony of several hundred plants was found on shaded ledges along the Baldy Trail, Santa Rita Mts., at an elevation of about 6500 feet."

The species differs from *B. acuta* (Brid.) Brid. in the generally larger size of the whole plants, longer stems and leaves, more revolute leaf margins, much longer capsules, and the longer, more twisted peristome teeth.

11. BARBULA BRACHYPHYLLA Sulliv., Rept. Pacific R. R. Surv. (35th Parallel) **4:** 186. 1856.

The typical form of this specis is very clear cut and distinct in its short leaves which may reach 1.5 mm. The leaves are also characterized by the very uniform areolation, the margins revolute from base to apex, and the sometimes obtuse apex. Furthermore, the peristome teeth are short and only slightly twisted. The short cells composing the ventral surface of the costa, and the dusty red peristome which becomes paler with age clearly ally this species with the *B. vinealis* complex. Many forms exist which are not altogether typical and which point to a still closer relationship to *B. vinealis*. Some of the material issued as *B. Bakeri* Card. & Thér. (q. v.) is clearly to be placed here in spite of the acute leaves, which may even end in a single pellucid cell exactly as in many forms of *B. vinealis*. *B. purpurea* C. Müll. is also most appropriately admitted to synonymy here. In the last analysis, then, we may consider *B. brachyphylla* simply as the most reduced form of the extremely variable *B. vinealis-B. cylindrica* complex.

12. *Barbula chrysopoda* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 57. 1892.

The original material upon which this species was based is absolutely typical *B. convoluta* Hedw. I have examined all the material named *B. chrysopoda* by Kindberg, from the National Museum in Stockholm and from the Canadian National Herbarium in Ottawa, and can find not even one characteristic by which this may be separated from *B. convoluta*. It is true that western forms of *B. convoluta* are apt to have larger perichaetial leaves with a better developed costa, but the difference is so subtle and so completely bridged by intermediate forms that there is no justification even for a form. The very long operculum attributed to *B. chrysopoda* (Kindberg, 1897) is just as characteristic of *B. convoluta* Hedw.

13. *Barbula circinnatula* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 56. 1892.

The original specimens, from Agassiz, British Columbia, upon which this name was based are fairly typical *B. cylindrica* (Tayl.) Schimp. The upper leaves on the stem are much longer, up to 5.0 mm. long, and conspicuously contorted and crisped when dry, and in other ways there is good agreement with *B. cylindrica*.

14. *Barbula cancellata* C. Müll., Flora **56**: 483. 1873.

I have seen type material of this species (from Texas) and can unhesitatingly pronounce it to be typical *B. Cruegeri* Sond. Even the multicellular axillary propagula are present on the type specimens. The remarkable peristome, in which the teeth are often cancellate or trabeculate at the base and appendiculate above, has led to the transfer of this species to *Dialytrichia* by Kindberg (1897), where it has been maintained by Brotherus (1909, 1924). *B. cancellata* has no relationship to *Dialytrichia*, however, especially in any gametophytic characteristics, but as already indicated, is really *B. Cruegeri*, which is more closely related to *B. unguiculata* Hedw. An interesting confirmation of this fact is that several specimens of *B. unguiculata* specially examined were found to have somewhat cancellate peristomes. The typically cancellate peristome of *B. Cruegeri* is exceedingly well demonstrated by Renauld and Cardot's "Musci Americae Septentrionalis Exsiccati" *No. 23*.

15. *Barbula Closteri* Aust., Bot. Gaz. **1**: 29. 1876.

The New Jersey specimens from which Austin described this species are very perplexing, as they are extremely depauperate and fragmentary. They approach *B. Cruegeri* closely enough, however, to allow us to unite the two species with reasonable safety. Several circumstances tend to substantiate this view. The Florida specimens of *B. Closteri* cited by Austin, although sterile, are definitely only poorly developed specimens of *B. Cruegeri*. Furthermore, a number of species thought to be restricted to the southern Coastal Plain have been discovered in New Jersey and on Long Island. Perhaps the best examples of this type of distribution are the recent discoveries of *Syrrhopodon texanus* Sull. (Cain, 1936; Grout, 1937) and *Syrrhopodon floridanus* Sull. (Wickes, 1937), on Long Island, New York.

Austin, in the original description of *B. Closteri*, suggested that it is "nearest to *B. convoluta*" in spite of the fact that some of his specimens bear archegonia, yet have absolutely no development of convolute-sheathing perichaetial leaves. Austin's misconception has been accepted and

brought into modern literature by Brotherus (1924) who includes it under the section *Streblotrichum*.

16. BARBULA CONVOLUTA Hedw., Sp. Musc. **120.** 1801.
B. chrysopoda C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 57. 1892.

This species is so common, widespread, and easily recognized that very little comment is necessary. In general, the American plants have shorter, fewer, and consequently less conspicuous perichaetial leaves than European specimens. However, the perichaetial leaves of American specimens tend to be more strongly costate.

17. BARBULA CRUEGERI Sond. in C. Müll., Syn. Musc. **1:** 618. 1849.
Tortula Cruegeri Mitt., Musc. Austr. Amer. **150.** 1869.
Barbula cancellata C. Müll., Flora **56:** 483. 1873.
B. Jooriana C. Müll., Bull. Torrey Club **5**(12): 49. 1874.
B. Closteri Aust., Bot. Gaz. **1:** 29. 1876.
B. Ravenelii Aust., Bot. Gaz. **2:** 89. 1877.
Tortula Closteri Aust., Bot. Gaz. **3:** 30. 1878.
Dialytrichia cancellata Kindb., Eur. & N.-Amer. Bryin. **291.** 1897.
Desmatodon Bushii Card. & Thér., Bot. Gaz. **37:** 366. 1904.

In spite of its frequency and wide distribution in the southern Coastal Plain, this species has remained seriously misunderstood, a statement vouched for by the extensive synonymy. It has a very superficial resemblance to the related *B. unguiculata* Hedw., which has resulted in a confusion of the two species by many competent workers, although they are really very distinct and there is even practically no overlapping in their geographical ranges. The smaller size, paler color, and red stems are characteristics which serve to distinguish *B. Cruegeri* in a sterile condition. The one absolutely unmistakable characteristic, yet one whose diagnostic value has not previously received recognition, is the presence of numbers of reddish, multicellular, axillary propagula, which will be found on the great majority of plants. On some specimens careful search is necessary to demonstrate the propagula, but on others the propagula are so numerous that the whole plant is given a reddish tinge. The sporophyte is characterized by its smaller size throughout; the capsule is shorter, paler and thinner walled than in *B. unguiculata*. The peristome is fugaceous and often strongly cancellate at the base. (See remarks under *B. cancellata* C. Müll.)

There is still some doubt in my mind as to the use of the name *B. Cruegeri*. Our plant, in its typical propaguliferous form, occurs throughout the hot tropical lowlands, especially in the West Indies. However, what is apparently another species, without propagula, from the high mountains

of Central and South America, is also called *B. Cruegeri*. I have not yet been able to see the type specimen of the species, from Trinidad, but rely for my use of the name on the words of Renauld and Cardot (1896), in reference to their "Musci Americae Septentrionalis Exsiccati," *No. 23:* "Ces échantillons de la Louisiane sont complètement identiques à ceux provenant de l'île de la Trinité, de l'Equateur et du Pérou." If, however, the type material of *B. Cruegeri* turns out to represent the tropical highland species, without propagula, then the propaguliferous species will have to bear the name *B. cancellata*, which antedates the long-established and well-known name *B. Jooriana*.

I have not been able to see the type material of *Desmatodon Bushii* Card. & Thér. from Missouri (1904), but can place it here without much question, from the description, especially from the remark that the peristome is to be compared with that of *B. cancellata*.

18. BARBULA CYLINDRICA (Tayl.) Schimp. in Ruthe, Hedwigia **12:** 46. 1873.

Zygotrichia cylindrica Tayl. in Mackay, Fl. Hib. **2:** 26. 1836.
Tortula cylindrica Lindb., Bot. Not. **1865:** 76. 1865.
Barbula flexifolia Hampe, Linn. **30:** 456. 1860.
B. subfallax C. Müll., Bot. Zeit. **20:** 338. 1862.
B. insulana Husn., Mouss. N. Ouest. **81:** 1873.
B. Beecheyi Lesq. in Watson, Bot. Calif. **2:** 372. 1880.
B. vinealis Brid. var. *cylindrica* Boulay, Mouss. Fr. **430.** 1884.
B. subcylindrica Broth., Bot. Centralbl. **44:** 387. 1890.
B. robustifolia C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 56. 1892.
B. circinnatula C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 56. 1892.
B. tortellifolia C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6** 56. 1892.
B. horridifolia C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 57. 1892.
B. pseudorigidula Kindb. in Macoun, Cat. Canad. Pl. **6:** 264. 1892.

This species, when well developed, is apt to be confused with none of our other species except, perhaps, *B. rubiginosa* Mitt., from which it is easily distinguished by the very different areolation, flexuous leaves, and the presence of a peristome. However, there is a very wide range of variation in *B. cylindrica*, as the extensive synonymy shows. Some of the specimens from Washington and British Columbia are much larger than any of the European specimens I have seen, whereas other specimens from farther south are much smaller and approach *B. vinealis* Brid. very closely. Apparently the fundamental differences between *B. cylindrica* and *B. vinealis* are as much quantitative as strictly qualitative, and no single

morphological characteristic is limited exclusively to either one species or the other. In general, the longer and more flexuous leaves, which are less strongly revolute, and the more papillose leaf cells, which are also smaller, will serve as identifying marks for *B. cylindrica*.

19. *Barbula decursivula* Kindb. in Macoun, Cat. Canad. Pl. **6:** 264. 1892.

The type material of this species, which the author compared to *B. brachyphylla* Sulliv., is without much doubt a somewhat reduced form of *B. fallax* Hedw., as is shown by the leaf shape, areolation, and particularly by the elongated cells which make up the ventral surface of the costa. The type collection of *B. decursivula*, which occurred "On earth, on rocks at Hector, Rocky Mountains, August 15th, 1890" thus represents one of the westernmost stations for *B. fallax*.

20. *Barbula Dieckii* Broth., Hedwigia **32:** 262. 1893. (*Didymodon Dieckii* Kindb., Eur. & N.-Amer. Bryin. **278.** 1897)

The type material of this species, from Washington, was compared to *Didymodon tophaceus* (Brid.) Jur. by Brotherus, but almost certainly belongs to *B. rubiginosa* Mitt. Although the type specimens are sterile, the plants have the characteristic colors, being yellowish-green above, but black below, and the leaves have the extremely uniform basal areolation of *B. rubiginosa*. The fact that the type locality is in Washington lends additional support to this view, as *B. rubiginosa* is most common in northern Washington and southern British Columbia.

21. *Barbula Donnellii* (Aust.) Lesq. & James, Manual. **128.** 1884.

The type material of Austin's *Tortula Donnellii*, from Florida, consists of a mixture of *Barbula agraria* Hedw. and *Desmatodon Sprengelii* (Schwaegr.) R. S. Williams. Dr. A. J. Grout has decided (*in litt.*) that Austin, already familiar with the *Barbula*, intended the new name for the *Desmatodon*, so that *Barbula Donnellii* should go into synonymy under *Desmatodon Sprengelii*. In spite of the statement in Lesquereux and James' "Manual" (1884, p. 128) that *B. Donnellii* is "Apparently a variety of one of the two preceding species" (*B. agraria* Hedw. and *B. Raui* Aust.), evidence for Dr. Grout's disposition of it is given by the remark in the "Manual" (l.c.) that *B. Donnellii* has "Leaves involute, . . . obscurely serrulate at the apex," since neither characteristic applies to *B. agraria*.

The material of *B. Donnellii* which has been issued in various exsiccati is almost generally *B. agraria*.

22. BARBULA EHRENBERGII (Lor.) Fleisch., Musci Archipelagi Indici Ser. IV, No. 161. 1901.

Trichostomum Ehrenbergii Lor., Abhandl. K. Akad. Wiss. Berlin **1867:** 25. 1868.

To Mr. Bartram must go the credit for recognizing this species within our range. Probably many specimens of it are to be found in the larger herbaria, misplaced under *Trichostomum* or *Didymodon*, both of which it resembles in several ways. In Mr. Bartram's herbarium are specimens from Texas, Oklahoma, and Missouri, which indicates that the species is apt to turn up elsewhere in the south and west.

The taxonomic position of this species has always been somewhat of a puzzle, until recently, when fruiting specimens of a very closely related plant were described from British Honduras (Steere, 1938a). Although the British Honduras material is enough different in gametophytic characteristics so that it cannot be safely thrown into *B. Ehrenbergii*, still it is sufficiently closely related to indicate the probable peristome structure. The peristome is quite typical of the genus *Barbula*, and exceedingly fragile, so that the teeth and even the low basal membrane are soon lost, giving deoperculate capsules a convincing appearance of being completely and naturally gymnostomous. That more typical material of *B. Ehrenbergii* behaves in a parallel manner is shown by the fact that the species has recently been placed in the gymnostomous genus *Hyophila* (Mönkemeyer, 1928). Of course, it cannot be placed in either *Trichostomum* or *Didymodon* (as has been proposed), because of the spirally twisted teeth.

23. *Barbula elata* Dur. & Mont. in C. Müll., Syn. Musc. **1:** 620. 1849.

This species, originally described from Algeria, has not yet been recognized in Europe; at least a search of the major monographic treatments of the European moss flora does not reveal even the name. In spite of the restriction of *B. elata* in the eastern hemisphere to Algeria, it has been reported from California, on the basis of Bolander's collections, by Lesquereux and James (1884), with the following remarks: "Near San Francisco (Bolander), mixed with the two preceding species [*B. virescens* Lesq. and *B. cylindrica* (Tayl.) Schimp.]. The more distant leaves, less open, recurved when moist, the stem-leaves ovate, decurrent at base, and especially the larger, broader capsule with longer, twice-twisted teeth, etc., separate this species from *B. vinealis*. The above description [i.e., of *B. elata* in the 'Manual'] made from the examination of a large number of specimens, slightly differs from that of Mueller. But this author has compared specimens and confirmed their identity with the foreign plant."

There is no real phytogeographic incompatibility in the discovery of an otherwise endemic Algerian species in California, as the climates of the two regions are essentially rather similar. The occurrence of *B. elata* in

the moister parts of Montana, Washington, and Oregon, reported by later workers, even as reliable as Brotherus (1893), would seem to be a bryogeographical impossibility, of course. Examination of specimens from the American northwest has shown them to be, beyond doubt, only *B. cylindrica* (Tayl.) Schimp. It is more than probable that Bolander's "*B. elata*" was the same, especially when Lesquereux and James' remark is recalled, that it was growing in mixture with *B. cylindrica* and *B. virescens*, the latter being a synonym of *B. vinealis*. Most of the specimens of "*B. elata*" from California, in various herbaria, are either *B. cylindrica* or *B. vinealis*.

The Herbarium of the New York Botanical Garden contains an interesting collection which bears on the packet, in ink, the following inscription: "*Tortula elata*, Dav. et Mont.—Algeria.—April 1848." Under the ink, however, is a faintly pencilled legend, apparently in the characteristic hand of Mrs. Britton, which sheds somewhat more light on our problem. In the first place, the pencilled spelling of the authorities is correct. In the second place, the last digit in the date, which is inked in as "8" is, in pencil, almost certainly a carelessly made "0." The reason for this careful documentation is that in the description of *Tortula elata* Dur. et Mont. (Montagne, 1849) which appeared at about the same time as (or earlier than?) Müller's description of *Barbula elata* Dur. & Mont., the habitat is given as "Ac rupas rivuli radices collis *Tournit* sublentis aprili 1840 in Algeria detexit cl. Durieu." Thus, the specimen in the New York Botanical Garden is almost conclusively proved to be a part of the type collection, or at least authentic material. Consequently, the determination of its status is a very critical matter. The leaves are long and flexuous, especially at the apex of the stem. The capsules are old, deoperculate, and have lost the peristome. Nevertheless, I do not hesitate in pronouncing this material to be a form of *B. cylindrica* (Tayl.) Schimp., without any reasonable doubt. The name *Barbula elata* must no longer be used for American specimens, and if the collection described above represents type material, the name cannot be used for the Algerian material, either.

24. BARBULA EUSTEGIA Card. & Thér., Bot. Gaz. **30**: 17. 1900.
B. perannulata Williams, Bull. N. Y. Bot. Gard. **2**(7): 358. 1902.

The type specimen of this species came from Cedar Creek, Latah County, Idaho. It has since been collected in Washington, Montana, and Utah. From the large number of specimens collected by Flowers and Garrett in Utah, especially in the Wasatch Mountains, it appears that this species is more common and abundant there than *B. convoluta*, from which it differs most conspicuously in the costate perichaetial leaves with a long, papillose apex or apiculus.

B. eustegia rather resembles the European *B. flavipes* Bry. eur., and it may eventually be necessary to place it there. However, the whole plant, in all its parts, is much smaller; furthermore, the perichaetium of *B. eustegia* is of fewer leaves, and much smaller in relation to the stem leaves, which may sometimes surpass it.

The sporophyte of *B. eustegia* is very similar to that of *B. convoluta* Hedw. Jones (1929) attempted to separate the two species in his key by the comparative lengths of the rostrate operculum, indicating that the operculum of *B. convoluta* is less than one half the length of the urn. Actually, however, in many specimens of *B. convoluta*, the operculum is longer than the urn, exactly as in *B. eustegia*.

25. BARBULA FALLAX Hedw., Sp. Musc. **120.** 1801.

B. acuminata Hedw., Sp. Musc. **117.** 1801.
B. sparsidens C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 54. 1892.
B. decursivula Kindb. in Macoun, Cat. Canad. Pl. **6:** 264. 1892.

This species has been very commonly considered to be widespread in our range from coast to coast, and every herbarium has its quota of specimens from the Pacific Coast states, especially California. In spite of this long-established idea, the specimens from the west coast attributed to *B. fallax* all belong actually to other species, usually *B. vinealis*.

B. fallax is really an eastern species, widespread from Nova Scotia to Virginia, west to Iowa and Minnesota. Farther west, the species seems much rarer and specimens are usually atypical, although a few reasonably typical specimens have come from Montana and Idaho. The two British Columbia collections described by Kindberg as two new species, *B. decursivula* and *B. sparsidens*, are much reduced, the first one so much that it is hardly recognizable as *B. fallax*.

Although *B. fallax* is rather variable, it (and its allies, *B. reflexa* (Brid.) Brid. and *B. michiganensis* Steere) may be easily separated from *B. vinealis* Brid., the species with which it is usually confused, by an easily observed and clear-cut characteristic, namely, the elongated cells (in surface view) composing the ventral surface of the costa. Furthermore, the peristome is of a clear, bright red, and does not become paler with age.

26. *Barbula flexifolia* Hampe, Linn. **30:** 456. 1860.

The type collection of this species (from California) is a small form of *B. cylindrica* (Tayl.) Schimp. Concerning *B. flexifolia*, Lesquereux and James (1884) very appropriately remark: "This and other species of the *B. vinealis* group are most difficult to separate, and their number may be either reduced or indefinitely increased." Renauld and Cardot (1896), in

the same vein, say of this species: "C'est une des nombreuses formes américaines du groupe des *B. vinealis* et *cylindrica*, que l'on à élevées au rang d'espèces, mais dont la valeur nous semble fort problématique. Une étude attentive de ce groupe conduira sans doute à y opérer de nombreuses réductions." In spite of many other remarks of the same sort which have appeared in the literature, none of the authors have taken the trouble to go ahead and straighten out the confusion which they suspect.

27. *Barbula gracilis* Schwaegr., Sp. Musc. Suppl. 1(1): 125. 1811.

The name *B. acuta* (Brid.) Brid. (Method. Musc. **96.** 1822) must be used for this species instead of *B. gracilis*, which is preceded by *Tortula acuta* Brid. (Musc. Recent. Suppl. **1:** 265. 1866).

28. *Barbula horridifolia* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 57. 1892.

The type specimens of this species, from "Damp rocks, near the whirlpool, west of the Columbia River, at Revelstoke, B. C." without doubt represent only a large form of *B. cylindrica* (Tayl.) Schimp. which has been so often redescribed under different names by Müller and Kindberg.

29. BARBULA ICMADOPHILA Schimp., Bry. Eur. fasc. **43,** suppl. II. 1850.

This species is recognized with any reasonable certainty in North America from only two specimens, in spite of several published reports and many collections so named in herbaria. The two collections which I should place here are R. S. Williams' *No. 143a* from Columbia Falls, Montana, and the admixture in Drummond's "Musci Americani" *No. 139*, issued as *T. fallax*. Although both specimens differ from European material in the somewhat papillose cells and shorter stems, they agree pretty well otherwise. In fact, Mitten (1878) has said of Drummond's collection just cited: " . . . fine specimens with fruit were in some sets of Drummond's Musci Americani, *No. 139*, as *T. fallax*, from banks of rivers near the Rocky Mountains." In the same place, Mitten reports "a few small barren stems" of *B. icmadophila* among other mosses at two stations in the extreme northernmost part of the Canadian Arctic Archipelago, at Floeberg Beach, Lat. 82°27′ N., and at Mushroom Point, Lat. 82°29′12″ N., on the north coast of Ellesmere Island. I have not seen these specimens from the English Arctic Expedition of 1875–1876, and so cannot express an opinion on them. For some reason, they are not in the Mitten Herbarium. now in the possession of the New York Botanical Garden.

30. *Barbula indigens* (Ren. & Card.) Ren. & Card., Bull. Soc. Roy. Bot. Belg. **36**(2): 176. 1897. (*Trichostomum indigens* Ren. & Card., Bot. Gaz. **4:** 50. 1896.)

Type material of this species, from Newfoundland, is almost certainly a much reduced form of *B. unguiculata* Hedw., with which it is compared by the authors. *B. unguiculata* apparently reaches its northern limit in eastern North America in Newfoundland, and since reduction in size is so typically concomitant with distribution in high latitudes, in species characteristic of temperate climates, it should not be taken as an excuse for the proposal of new species. At the other end of our geographical range, Cardot made the curious error of applying the name *B. indigens* to rather typical specimens of *B. Cruegeri* Sond. collected at Columbia, Texas, and to unquestonable *B. unguiculata* from Missouri. This extremely disjunct geographical range should have aroused suspicion as to the validity of the species, even before a critical examination of authentic material.

31. *Barbula insulana* (DeNot.) Husn., Mouss. nord-ouest **81.** 1873.

This name, which is a synonym of *B. cylindrica* (Tayl.) Schimp., has been applied to American plants and so has appeared a few times in the literature concerning them.

32. BARBULA JOHANSENII Williams, Rept. Canad. Arct. Exped. 1913–18. **4**(E): 4. 1921.

As this species is known only from the nearly inaccessible type locality, Murray Point, Victoria Island, Arctic Northwest Territory, Lat. 68°40′ N., on dolomite cliffs (Frits Johansen, March 25, 1916), and only from one small collection, it must be admitted to our flora with some question. However, it seems to be distinct, although closely related to *B. acuta* (Brid.) Brid., and certainly differs from every other species in the genus in the swollen, caducous apex of the costa, which must serve in some way for vegetative reproduction.

33. *Barbula Jooriana* C. Müll., Bull. Torrey Bot. Club **5**(12): 49. 1874.

The type specimen (from Baton Rouge, Louisiana) of this species has been seen, through the kindness of the Botanical Museum, Berlin-Dahlem, Germany. It represents, without question, *B. Cruegeri* Sond., since axillary propagula are present, although not particularly well developed. Many bryologists from the time of the Lesquereux and James' "Manual" (1884) on have considered *B. Jooriana*, under which name the majority of specimens of *B. Cruegeri* pass, most closely related to *B. unguiculata* or even not separable from it.

34. *Barbula lanceolata* Hedw., Sp. Musc. **119.** 1801.

In the original description, according to which the type collection was found growing "Terrestris Lancastriae in Pensilvania," Hedwig gave no

indication as to what he considered the affiliations of his new species. Cardot (1899), however, has examined the original material and pronounced it to be a form of *B. unguiculata* Hedw.

35. *Barbula lateritia* Kindb., Eur. & N.-Amer. Bryin. **264.** 1897.

Type material of this species, as nearly as the type material of any of Kindberg's species may be ascertained, although sterile, is a short form of *B. vinealis* Brid., which approaches *B. brachyphylla* Sulliv. rather closely, especially in the leaf margins revolute from the base nearly to the apex.

36. *Barbula melanocarpa* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 54. 1892.

The type material of this species, from Yale, B. C., certainly represents *B. rubiginosa* Mitt. The complete lack of any peristome, the absolutely characteristic basal areolation of the leaf, and the curious, almost metallic blackness of the old leaves identify it beyond question.

37. BARBULA MICHIGANENSIS Steere in Grout, Moss Fl. N. Amer. **1**(3): 180. 1938.

This species, although known only from the type locality on the south shore of Lake Superior, is represented by several collections made at different times, and seems distinct enough to necessitate recognition. The very thick-walled, seriate cells of the lamina, the elongated cells of the ventral surface of the costa, as well as the whole general appearance of the plant, especially the catenulate leaf arrangement when dry, all point to a definite relationship with *B. fallax* Hedw. However, the clasping, erect leaf base, with only the apex reflexed- and erect-spreading, is very different from the widely reflexed-spreading leaf arrangement in *B. fallax* and, still more, in *B. reflexa* (Brid.) Brid. Also, the cells are thicker walled, less papillose, and much more conspicuously arranged in parallel rows than usual in *B. fallax*. The really unique feature, however, is the presence in large numbers of reddish, spherical, multicellular propagula in the axil of each leaf, because this type of propagulum is not known in any other of our American species, nor have propagula of any type been reported for either *B. fallax* or *B. reflexa*.

38. *Barbula oenea* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 55. 1892.

An examination of the sterile type specimen of this species shows it to be almost certainly a *Didymodon*, as the authors themselves suspected. Just what species is represented would be very difficult to say, however,

as the type material is not only very scanty, but also poorly developed. It was growing, according to the authors, on soil subject to inundation, a variable habitat which has left its mark upon the specimens. This name should be discarded altogether, without hesitation.

39. *Barbula perannulata* Williams, Bull. N. Y. Bot. Gard. **2**(7): 358. 1902.

The original material of this species came from Montana and Idaho. An examination of the type specimens, the original description, and Williams' illustrations leaves no reasonable doubt that it is a question of *B. eustegia* Card. & Thér., which was described from the same general region only two years earlier.

40. BARBULA PLATYNEURA C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 52. 1892.

In this plant, C. Müller and Kindberg seem actually to have found a valid new species. After seeing specimen after specimen of well-known and long-established species wrongly identified and badly confused, or, still worse, proposed as innumerable new species, one develops a certain distrust of Kindberg's reliability. However, although this species is still known only from the type specimen, it is different from any other species and is seemingly the American counterpart of the European *B. Hornschuchiana* Schultz, from which it differs in its tendency toward a more obtuse leaf apex and the lack of spiral twisting of the leaves when dry. From *B. spiralis* Schimp., of the arid southwest, it differs in smaller size, more acute leaves, and the much shorter basal leaf cells.

41. *Barbula pseudorigidula* Kindb. in Macoun, Cat. Canad. Pl. **6**: 264. 1892.

The type material of this species is without much doubt a form of *B. cylindrica* (Tayl.) Schimp. with which it agrees in the flexuous leaves, spreading when moist, and in "the peristome pale and distinctly contorted." In just these same characteristics it differs from *B.* (*Didymodon*) *rigidula*, which also has the upper leaf margins thickened.

42. *Barbula purpurea* C. Müll., Flora **58**: 78. 1875.

Sullivant and Lesquereux's "Musci Boreali-Americani" *No. 135* (Ed. II), issued as *B. brachyphylla* Sulliv., is in part the type material of this species. I have seen several separate packets of *No. 135*, from different sets, as well as the actual material selected out by Müller, from his herbarium. The species is apparently only a habitat variation of *B. brachyphylla* and not enough different to justify separation from it.

43. *Barbula Raui* Aust., Bull. Torrey Bot. Club **6**: 43. 1875.

Although this species has been considered as valid and distributed in exsiccati even since 1930 (for instance, *No. 194* of Grout's "North American Musci Perfecti"), I am obliged, after an examination of the type specimen, to agree with Mrs. Britton (1913) and Williams (in herb.) that it is too close to *B. agraria* Hedw. for recognition, and so should go into synonymy under *B. agraria*.

44. *Barbula Ravenelii* Aust., Bot. Gaz. **2**: 89. 1877.

The original specimens upon which this species was based, although somewhat reduced, are typical *B. Cruegeri* Sond., even to the well-developed axillary propagula. *B. Cruegeri* must be rare in Georgia, because, although the type specimen of *B. Ravenelii* was collected prior to 1877, no other specimens from Georgia have found their way into the larger herbaria.

45. *Barbula recurvifolia* Schimp., Coroll. Bry. Eur. **33.** 1855.

This name is preceded by *B. reflexa* (Brid.) Brid. (Method. Musc. **93.** 1822), which, then, is the proper one to use.

46. BARBULA REFLEXA (Brid.) Brid., Method. Musc. **93.** 1822.

This species, subspecies, variety, or form, as it has been variously considered by as many authors, is very closely related to *B. fallax* Hedw., and has much the same geographic range. It is not particularly variable, and differs fairly consistently from *B. fallax* in its redder color, more papillose leaf cells, and more strongly recurved or even squarrose leaves. As to the proper category in which to place this moss, it is probably best considered a "small" species or a subspecies of *B. fallax*.

47. *Barbula rigens* Card. & Thér., Proc. Wash. Acad. Sci. **4**: 305. 1902.

The type material of this species, from Alaska, consists of only a few sterile stems, which, although puzzling, seem to represent an elongated, underdeveloped form of *Didymodon recurvirostris* (Hedw.) Jennings (*D. rubellus* Bry. eur.). This view is based upon the very typical coloration, the much elongated basal cells and the costa shortly excurrent into a minute, pellucid apiculus. The apical teeth are very poorly developed, however, although they may commonly be lacking or poorly developed in specimens from more Arctic regions.

48. *Barbula rigidula* (Hedw.) Milde, Bryol. Siles. **118.** 1869.

This species, although closely related to *Barbula* in appearance and habitat, is to be kept in the almost completely synthetic genus *Didymodon* (Steere, 1938c) as long as it is maintained, on the basis of the nearly

straight peristome teeth and the fact that it is the type species of Hedwig's genus *Didymodon*. It is worth remarking here that, although Mitten (1867) is almost universally given credit for the transfer of this species to *Barbula*, he, in the place always cited, speaks only of "*T. rigidula*," although he does make the following qualifying remark at the beginning of his paper: "In Britain these mosses are, for the most part, called *Tortulas*, but elsewhere they are found in Bryological works, generally under the synonymous name of *Barbula*, which later designation they may probably eventually retain when the present chaotic state of the extensive family, of which they form a part, shall have been reduced to order on some more natural plan; a few species have been placed in *Trichostomum* and *Didymodon*, from the importance which has been placed in the length of the peristome teeth." The expression of this viewpoint can hardly be construed as establishing a valid new combination, and as Mitten nowhere uses "*Barbula rigidula*" he can not very logically be cited as the authority for it. Milde, in the work cited above, seems to have first used this combination, insofar as I can discover, and so it should be attributed to him, if the species be retained in *Barbula*.

49. *Barbula robustifolia* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 56. 1892.

The type specimens of this species, from Vancouver Island, are simply a robust form of *B. cylindrica* (Tayl.) Schimp. into which it should be thrown.

50. BARBULA RUBIGINOSA Mitt., Journ. Linn. Soc. Bot. **8**: 27. 1865.
Barbula subicmadophila C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 53. 1892.
B. melanocarpa C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 54. 1892.
B. Dieckii Broth. in Röll, Hedwigia **32**: 262. 1893.
Didymodon Dieckii Kindb., Eur. & N.-Amer. Bryin. 278. 1897.

Although this species seems to be especially common along the Columbia River, it is widespread in Oregon, Washington, Idaho, Montana, and southern British Columbia. It has often been confused with *B. cylindrica* (Tayl.) Schimp., quite unreasonably. Fertile specimens are absolutely unique in their complete lack of any peristome. Sterile specimens are also easily recognized by the more decurrent leaves, which are less contorted when dry and less flexuous when moist, as well as by the extremely uniform, short basal leaf cells, which may actually be wider than long. The relationships of this species in the genus *Barbula* are very obscure. I find myself somewhat in sympathy with Kindberg (1897), who placed it in *Didymodon*. Of course, the total lack of a peristome and the peculiar areo-

lation are known otherwise in neither *Barbula* nor *Didymodon*. If these characteristics are of any real taxonomic importance, then perhaps it may eventually be necessary to erect a new genus to contain this species.

51. *Barbula Saundersii* Card. & Thér., Proc. Wash. Acad. Sci. **4:** 304. 1902.

The original material upon which this species was based, from southern Alaska, "in habit recalls the smallest forms of *B. unguiculata* Hedw." The characteristic dirty green color, the basal areolation of the leaf, and the costa papillose on the back substantiate the authors' suspicion that this might represent *B. unguiculata*. The shape of the leaf is rather different, as the authors point out. However, in a species as polymorphic as *B. unguiculata*, variants of this sort hardly merit recognition, even with the rank of a form. This is especially true of specimens such as these, from the extreme northern limit of the geographic range, where the climate may naturally be expected to influence a species of temperate regions.

52. *Barbula semitorta* Sulliv., Rept. Pacific R. R. Survey (35th Parallel) **4:** 186. 1856.

The Californian specimens upon which this name is based are clearly a form of *B. vinealis* Brid., which, as the author states, accompanies it.

53. *Barbula sinuosa* (Wils.) Jaeg., Adumb. **1:** 286. 1873.

In the first place, this species is probably not a *Barbula* at all: at least that is my conclusion after studying several European collections. In the second place, the species, whether or not it belongs to *Barbula*, apparently does not occur in North America, in spite of published reports to the contrary by Kindberg and others.

54. *Barbula spadicea* (Mitt.) Braithw., Brit. Moss-Fl. **1:** 266. 1887.

This species is not particularly closely related to, but often confused with *Didymodon rigidulus* Hedw., and the remarks which have been made concerning the latter species also apply here. The straight or nearly straight peristome teeth force its inclusion in the genus *Didymodon*, for the present at least. For the sake of exactitude in citation, however, it might be mentioned that in the original description this species was proposed unequivocally and unmistakably as a *Tortula* by Mitten (1867). Nevertheless, most bryologists have credited Mitten with the authorship of the name *Barbula spadicea*, although citing the place of publication of his "*T. spadicea*, n. sp."; perhaps because of his qualifying remarks already quoted under *B. rigidula*. So far as I can find, Braithwaite, as cited above, was the first to use the actual combination *Barbula spadicea*, although he himself indicated Mitten as the author.

55. *Barbula sparsidens* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 54. 1892.

The authors say of this species in the original description: "Allied to *B. fallax*, but differing principally in the peristomial teeth, spreading, loosely, and not spirally twisted." A careful examination of the type specimens, from "Along the west side of the Columbia River, at Revelstoke, B. C." has shown them not only to be reasonably typical *B. fallax* Hedw., but also to be from the westernmost outpost of that species. When the operculum is first removed or the teeth are moistened, they assume the characteristic spiral contortion. In old, dry peristomes the teeth spread out, giving the false appearance of being untwisted. The clear, deep red color of the peristome and the elongated cells composing the ventral surface of the costa complete the identification of this species with *B. fallax* beyond question.

56. BARBULA SPIRALIS Schimp. in C. Müll., Syn. Musc. **1**: 622. 1849.

Concerning the distribution of this species, Bartram (1927) says: "This species is apparently quite common in the elevated districts of central Mexico and is certainly not uncommon in Arizona where it has been collected in a number of localities, usually on dry banks in the foothills of the border mountain ranges. Collections by Mr. Holzinger in New Mexico and by Mr. C. R. Orcutt in western Texas indicate that the species probably occurs throughout the arid southwest at elevations around 5000 feet."

From *B. platyneura* C. Müll. & Kindb., its closest relative, *B. spiralis* is separated easily by the larger size and less acute leaves, but especially by the much longer basal leaf cells. It seems to be related to the European *B. revoluta* Brid., but differs in the much larger size and undifferentiated perichaetial leaves. I have not seen any material with sporophytes from our range.

57. *Barbula stricta* Hedw., Sp. Musc. **119**. 1801.

Cardot (1899) examined the type material of this species, which, according to the original description, came from "Lancaster Pensilvaniae, terrestris," and has pronounced it to be a robust form of *B. unguiculata* with tall stems.

58. *Barbula subandreaeoides* Kindb., Rev. Bryol. **32**: 36. 1905.

The original material upon which this name was based, from the western slope of the Rocky Mountains, British Columbia, rather definitely represents a form of *Andreaea Rothii* Web. & Mohr, a conclusion which Dr. Sharp has confirmed.

59. *Barbula subcylindrica* Broth., Bot. Centralbl. **44:** 387. 1890.

Through the kindness of Dr. K. Linkola, of the Botanical Institute of Helsinki University, I have seen type specimens from Brotherus' Herbarium. In spite of the slight deviations from typical *B. cylindrica* (Tayl.) Schimp. noted by the author, the type material falls well within the range of variation of the American forms of *B. cylindrica*.

60. *Barbula subfallax* C. Müll., Bot. Zeit. **20:** 338. 1862.

The type material of this Californian species, which has been seen through the kindness of the Berlin-Dahlem Botanical Garden, clearly represents a somewhat reduced form of *B. cylindrica* (Tayl.) Schimp., in spite of the comparison with *B. fallax* Hedw. by the author. The leaves are crowded, longer, and flexuous at the stem apex, the leaf margin is not revolute above the middle, and in all other critical features it agrees with *B. cylindrica*.

61. *Barbula subgracilis* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 53. 1892.

Although the authors consider this species "allied to *B. gracilis*," several of the characteristics mentioned in the original description distinctly contradict such an alliance. For instance, the "leaves when dry subcrispate, when moistened squarrose, curved from the ovate base" are not at all characteristic of *B. acuta* (Brid.) Brid., but of the *B. vinealis* Brid. series. A study of the type specimens has shown them to represent *B. vinealis*.

62. *Barbula subicmadophila* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 53. 1892.

The original material of this species, from "dry rocks, but which are covered at high water, at Yale, B. C." is certainly *B. rubiginosa* Mitt. The complete lack of a peristome, in the first place, is the most positive means of identification.

63. *Barbula tortellifolia* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 56. 1892.

The type specimens upon which this species was based, from various parts of British Columbia, are clearly the same large form of *B. cylindrica* (Tayl.) Schimp. which these authors chose to redescribe so many times as different species.

64. *Barbula Treleasei* Card. & Thér., Proc. Wash. Acad. Sci. **4:** 305. 1902.

In spite of the authors' comment on this species: "It differs from *B.*

vinealis Brid., and allied forms, by the much shorter leaves," the type material, from Juneau, Alaska, is rather typical *B. vinealis*, even to the single pellucid cell at the apex of the leaf.

65. BARBULA UNGUICULATA Hedw., Sp. Musc. **118.** 1801.

Barbula indigens (Ren. & Card.) Ren. & Card., Bull. Soc. Roy. Bot. Belg. **36**(2): 176. 1897.

B. Saundersii Card. & Thér., Proc. Wash. Acad. Sci. **4:** 304. 1902.

The typical American form of this extremely common, widely distributed, and variable species differs from the typical European form in the less strongly excurrent costa, which forms a shorter mucro, and in the less hyaline basal cells, as well as in more subtle and less easily defined ways. Yet the two forms are united by a whole series of intergrading forms. Many variants, whose names reveal their nature, have been given formal recognition at various times in the past, as *cuspidata, apiculata, microcarpa, obtusifolia, polycarpa, fastigiata*, etc. All these merge imperceptibly with the typical form, however, and are of no real taxonomic value, even as forms.

66. BARBULA VINEALIS Brid., Bryol. Univ. **1:** 830. 1826.

Tortula vinealis Spruce, Hook. Journ. Bot. **4:** 194. 1845.

Barbula semitorta Sulliv., Rept. Pacific R. R. Surv. (35th Parallel) **4:** 186. 1856.

B. virescens Lesq., Trans. Amer. Phil. Soc. **13:** 4. 1865.

B. cylindrica (Tayl.) Schimp. var. *vinealis* Lindb., Musc. Scand. **22.** 1879.

B. brachyphylla Sulliv. var. *angustifolia* Kindb. in Macoun, Cat. Canad. Pl. **6:** 55. 1892.

B. lateritia Kindb., Eur. & N.-Amer. Bryin. **264.** 1897.

B. Treleasei Card. & Thér., Wash. Acad. Sci. Proc. **4:** 305. 1902.

This is, without doubt, the most variable species of *Barbula*, and is represented, especially in California, by a perplexing series of races and habitat forms, too many of which have been proposed as species. Sullivant's *B. brachyphylla*, which apparently represents the most reduced state of *B. vinealis*, usually with a somewhat blunt leaf apex and with the whole leaf margin revolute, is distinct enough for recognition as a species or subspecies, in its typical form. Puzzling intermediate forms do occur, however. In the other direction, the more robust forms of *B. vinealis* intergrade to some extent with *B. cylindrica* (Tayl.) Schimp. Yet the total range of the three "species" is too great to enable us to lump them under one name. Perhaps further study will uncover better morphological and qualitative distinctions between them.

B. vinealis has long been confused with *B. fallax* Hedw., with the result that in every herbarium there are too many specimens labelled "*B. fallax*," especially from the Pacific Coast. Although there are many forms of *B. vinealis* which almost exactly duplicate the macroscopic habit of *B. fallax*, the geographical ranges hardly overlap, and under the microscope the two species are very distinct. The leaf cells of *B. vinealis* are ordinarily much less papillose and less thickened, and the peristome teeth are rarely a deep, clear red, but have a dusty or glaucous quality, and become much paler or even completely white with age. An inspection of the ventral (upper) surface of the costa under the microscope will separate the two species without any question, for in *B. vinealis* the cells are short, appearing as a continuation of the leaf blade across the costa, whereas in *B. fallax* the cells are much narrower and elongated, very different from those of the lamina.

It is interesting to read the comments made by earlier bryologists on the American species of *Barbula*, and to discover what sort of specific concepts they held, especially with reference to the perplexing *B. vinealis* group. Lesquereux (1865) was apparently distinctly puzzled, as his remarks show. Concerning *B. vinealis* Brid., he says: "Very common and variable around San Francisco. Var. α has the ramification, form of leaves, etc., of *Barbula vinealis;* but the operculum and peristome of *Barbula flexifolia*. Var. β *flaccida* Bry. Eur. has the capsule and operculum of *Barbula vinealis*, and the long-linear, lanceolate, canaliculate, open-reflexed, loosely imbricated leaves of *Barbula flexifolia*. This variety is apparently the equivalent of *Barbula elata* C. Müll." On the basis of these observations, Lesquereux would have been perfectly justified in reducing *B. flexifolia* and *B. elata* at once to synonyms of *B. vinealis* Brid. var. *flaccida* Bry. Eur., which in itself is, of course, only a synonym of *B. cylindrica* (Tayl.) Schimp. Instead of following this practical course, he maintained both species in the "Manual" (1884), which, as a result of this same uncritical procedure in all groups, is essentially only a compilation. After admitting the complexity of *B. vinealis*, he went on and described (1865) two new species of *Barbula*, *B. virescens* and *B. artocarpa*. That Lesquereux himself had serious doubts concerning the validity of his new species is clearly demonstrated by his remarks. Of his *B. virescens* he says: "This species is intermediate between *Barbula flexifolia* Hmp. and *Barbula semitorta* Sul., two species already closely related." Of *B. artocarpa*, which is clearly based on *B. vinealis*, he says: "Except for its pretty large annulus, this species would agree with *Barbula gracilis* Schw., which it exactly resembles by the ramification, the form of the leaves and of the capsule. It is also nearly related to *B. subfallax* C. Müll. [*B. cylindrica*], which has also

no annulus, and a shorter basilar membrane." No good is done by the addition of new species whose value the author himself doubts, as shown by his final statement that "It is, indeed, with some misgiving that I add two new species to this group of *Barbulae* already too much divided. But I have no other alternative but to do this, or to recall as mere varieties, a number of forms considered as species by other authors, and whose characters are of the same kind and no more definite." A few years later, Lesquereux (1868) was still undecided in his treatment of the *B. vinealis* series, saying: "The forms of this section of *Barbula* found in California are so numerous, that it will be necessary to reduce them to a few species, or to make a monograph of them, embracing more than one dozen species." Still later (1884), he says (with reference to *B. flexifolia* Hampe): "This and other species of the *B. vinealis* group are most difficult to separate, and their number may be either reduced or indefinitely increased." Unfortunately, the latter choice was made by most bryologists during the next quarter century.

When as conscientious a worker as Lesquereux recognized species other workers had based upon habitat forms and proposed new species based upon characteristics which he himself considered unreliable, it is fortunate for American bryology that Bolander's Californian mosses were not sent to Kindberg.

67. *Barbula virescens* Lesq., Trans. Amer. Phil. Soc. **13:** 4. 1864.

The original material from California, upon which this species was based, is undoubtedly a form of *B. vinealis* Brid., as just pointed out under that species.

68. *Barbula Waghornei* Kindb., Eur. & N.-Amer. Bryin. **264.** 1897.

The type specimens of this species, from Newfoundland, have an excurrent costa, as the author noted, and in addition show two other characteristics which escaped the author, but which allow the material to be identified without the least doubt as *Didymodon rigidulus* Hedw. The leaf margin is characteristically bistratose above and there are groups of the typical spherical, multicellular, stalked propagula present in the axils of the leaves.

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Pollen Longevity of Ginkgo[1]

EARL H. NEWCOMER

(WITH FOUR FIGURES)

Pollen was collected May 15, 1937, from a male tree of *Ginkgo biloba* growing near the campus of The Pennsylvania State College. The primary purpose of the collection was to secure an adequate amount of pollen for germination studies by a method devised by the author for the pollen of Angiosperms (*2*). The presence of functional chloroplasts in the male gametophyte of *Ginkgo* seemed to offer favorable material for observing the fate of the plastid through a critical part of the life cycle. However, all attempts to germinate the pollen failed, although efforts were made at regular intervals for a period of more than four months with a variety of media and stimulatory substances. The apparent continued viability of the pollen for so long an interval suggested the experiment to determine its longevity.

Horsford (*1*) kept the pollen of *Lilium auratum* viable for a year by simply wrapping it in two or three sheets of paraffin paper and storing it in a warm dry place. More recently, Pfeiffer (*3*) made a detailed study using a variety of salts and acids to control humidity in conjunction with various temperatures and pressures and succeeded in keeping the pollen of *Lilium* viable for a period of fourteen months.

The *Ginkgo* pollen, which had been intermittently kept in a refrigerator at 7 degrees C. when not on the author's desk, was placed in a desiccator over powdered $CaCl_2$ as shown in figure 4, and returned to the refrigerator until the following spring. On May 2, 1938, the pollen was applied with a camel's hair brush to the young ovules of a female *Ginkgo* tree. The young ovules were bagged before pollination and subsequently for more than a month—a precaution doubtless unnecessary as the nearest male tree is a quarter of a mile distant to the leeward and wind pollination has never been observed on this tree.

That the pollen was still viable is attested by the accompanying figures of fruits taken at intervals throughout the summer. Sections of these young developing ovules and embryos show normal development.

This same tree was hand pollinated on May 15 the preceding year and cytological studies demonstrated fertilization occurring between the 5th and 20th of September. Counting this four-month period between pollination and fertilization, the pollen maintained its viability for a period of nearly sixteen months.

[1] Contribution from the Department of Botany, Michigan State College.

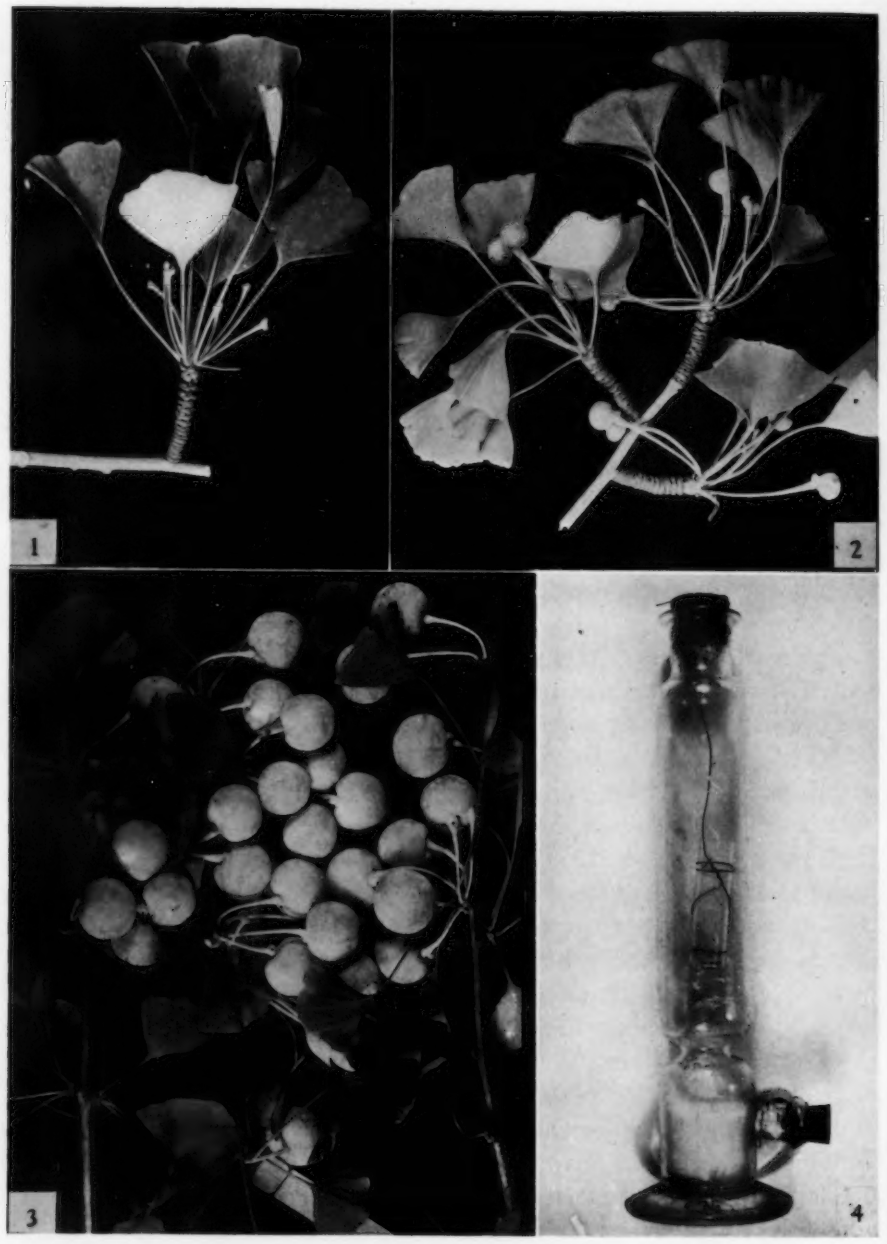

Fig. 1. Young ovules of *Ginkgo biloba* at time of pollination. May 2, 1938.

Fig. 2. Developing ovules on June 20, 1938. Abortive or unpollinated ovule in center of field.

Fig. 3. Mature fruit at time of final collection. Oct. 1, 1938.

Fig. 4. Desiccator used for storage of pollen. Vial containing pollen suspended from cork by copper wire over $CaCl_2$.

Actual percentage germination studies of viable pollen were impossible to make, but microscopic examination of the pollen at time of pollination revealed less than 1 per cent of shrivelled pollen. Indeed, present examination shows the pollen grains to be but slightly shrunken and when mounted in a drop of water, they immediately expand to their normal size and, with the exception of the almost complete disappearance of the chloroplasts, appear normal. Brownian movement of small bodies which may be the remnants of the plastid stroma, is conspicuous. The prothallial, tube and generative nuclei are still normal in appearance and position. An adequate amount of pollen remains for further experiment in the spring.

It is a pleasure to acknowledge the assistance of Professor L. O. Overholts, of The Pennsylvania State College, for the photographs, and of Dr. C. C. Wernham, of the same institution, for the final fruit collections.

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INDEX TO AMERICAN BOTANICAL LITERATURE

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